Sealworms (*Pseudoterranova decipiens*) in shorthorn sculpin (*Myoxocephalus scorpius*) from the outer Oslofjord

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Abstract

Sealworms, *Pseudoterranova decipiens,* are found in several fish species, and generally have a high prevalence in cod (*Gadus morhua*) and sculpins (*Myoxocephalus scorpius*). In the outer Oslofjord the final host is common seals (*Phoca vitulina* Linne, 1758), and here there are two colonies of these seals: a small population of 150 – 400 individuals in the outer Hvaler skerries in Norway and a large population of more than 2000 individuals in the Koster archipelago in Sweden. A feature of the sealworm life cycle in these habitats is that sculpins (*Myoxocephalus scorpius*) act as an important transmitter from invertebrates to cod. Heavily infested seals have eaten cod which have consumed heavily infected sculpins. The purpose of this project was to compare the sculpins found from Hvaler and Koster in order to investigate the effect of the number of common seals on the infection levels in sculpins.

We investigated 107 sculpins from the Hvaler Islands in 2009 and 161 sculpins from the Koster archipelago in the 1990's. Females constituted slightly less than 70 % of the samples and had a significant different age structure than males. While the females were between 1.5 and 4.5 years old, the males achieved one year less: 1.5 – 3.5 years. All fish were between 12 and 29 cm. Females were approx. 5 cm longer than males.

In Hvaler around 25 % of the sculpins were infested by sealworms and the number of sealworms per fish varied between 0 and 4. On average, the number of sealworms per investigated fish (abundance) was 0.4 in Hvaler, and the number of sealworms per infested fish (intensity) was 1.6. In Koster around. 85 % of the sculpins were infested by sealworms and the number of sealworm per fish varied between 0 and 34 with the exception of 102 sealworms in one female. On average, the number of sealworms per investigated fish was 6.4, and the number of sealworms per infested fish (intensity) was 7.5.

There was no correlation between the number of sealworm and weight of the fish. In the Hvaler Islands, with few common seals, the number of sealworms per fish followed a Poisson distribution. In the Koster Islands with many common seals, the number of sealworms per fish had a large deviation from the Poisson distribution. In addition to the abundance of seals, the diet of sculpins may contribute to the observed differences in the distribution of sealworms in sculpins in the two areas.

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1 Introduction

This study is one part of a larger student project on sealworms conducted by Karl Inne Ugland at the Marine Biology Research Program of the Department of Biology at the University of Oslo. Previous studies have revealed that the degree of infestation by sealworms (*Pseudoterranova decipiens*) seems to be rather independent of the number of common seals in the outer Oslofjord. Large samples of some fish species and stomachs of common seals have been collected by several students under the leadership of Morten Bronndal in the last years. I was part of the team doing fieldwork in autumn 2010 at Torbjørnskjær in southern Norway and near Finnøy in the west coast of Norway. Together with the other participating students I took part in identifying the stomach contents of the seals and identifying parasites from the stomach, lung and heart. We also preserved the nematodes for future investigation. Bjørn Berland from the University of Bergen taught us the techniques for fixing and identifying the nematodes from fish and seals. In addition we used the otoliths for age determination of fish. The project is ongoing and more results will be presented in 2012.

The third stage of the parasitic sealworm *Pseudoterranova decipiens* (Krabbe 1878) is known to infect over 75 different fish species in the North Atlantic waters (McClelland 1990; Jensen et al. 1994a; Desportes & McClelland 2001). It has been a nuisance for fishermen since many commercially important fish species, including codfish and flatfish, are frequently highly infected. Infection levels in noncommercial species like sculpin (*Myoxocephalus scorpius*, Linnaeus 1758) have been much less studied, despite the fact that sculpin is one of the most heavily infected species in the vicinity of seal haul-outs in the North-East Atlantic (Háuksson 1992; Jensen & Andersen 1992; Jensen 1997a). In general, sealworms have the greatest prevalence (percentage of infected individuals) and abundance (average number of worms in the host population) in benthophagous and demersal species such as cod (*Gadus morhua*), cusk (*Bromse Bromse*), sculpins and

flatfishes (McCelland et al. 1990; Jensen & Andersen 1992; Jensen 1997a). Since a large fraction of coastal cod may be heavily infected, the sealworm is also called the codworm.

While larval stages of *P. decipiens* have demersal fish and benthic invertebrates as intermediate hosts, maturation takes place in the stomachs of seals (McCelland et al. 1990). In the North-East Atlantic the most important final hosts are grey seals (*Halichoerus grypus* Fabricius 1791) and harbour seals (*Phoca vitulina* Linne, 1758). Mc Clelland (1980) found that the sealworm has better survival, growth and fecundity in grey seals than in common seals. Therefore grey seals are considered to be better final hosts and they are known to carry considerable abundances of sealworms; frequently hundreds of individuals.

In the outer Oslofjord it is harbour seals that form the main hosts since grey seals only rarely occur in this area. At Torbjørnskjær the distribution of the sealworm larvae in fish is locally restricted to the area around the seal skerries. Jensen and Idås (1992) found that sealworm infection in cod is positively correlated with seal numbers while it is inversely related to the distance from haul-out skerries at Torbjørnskjær. Further, it is suggested that sculpins play a major role as transmitter of sealworms from invertebrates to cod (Aspholm et al. 1995; Lunneryd et al. 2001). Since harbour seals seem to avoid eating sculpins, a harbour seal containing a large number of sealworms is assumed to have eaten cod that have eaten sculpins. However, some studies indicate that sculpin is directly a part of harbour seals diet (Pierce et al. 1990; Háuksson 1992), but the otoliths of small fish species are rarely found because of seals heavy digestion (Jensen 1997a). An experimental study by Jensen (1997b) found that sealworm larvae have a low survival when transferred from sculpin to cod, thus indicating that a cod might not play a major role in the sealworm life-cycle. Theoretically a seal has to eat nearly 20 times as many cod as sculpins to reach comparable infection sizes. In addition to the species, the size of the fish and abundance is important in the transmission of the sealworm larvae to the next host. Some studies have claimed that larger and older fish have higher sealworm infection levels (des Clers 1989; Jensen et al. 1994b).

Although many studies have described the major transmission routes of the sealworms in Norwegian waters (Figure 1.1), further investigations are needed to examine the relative importance of age and size of the intermediate host in the transmission of sealworm to the next host. In addition, the abundance of seals in the area plays important role in shaping the distribution of sealworms in fish population (McCelland et al. 1983; Bjørge 1985; Scott & Dobson 1989). However, several studies have shown that the rate of infection in fish seems to be independent of the abundance of seals in the area after a certain threshold (Desportes & McClelland 2001; Lunneryd et al. 2001). This can be further investigated by comparing sealworm infection levels in sculpins in Hvaler, where the abundance of seals is low and in Koster, where the abundance of seals is high.

In order to achieve a better understanding of the factors leading to the different sealworm infection patterns in sculpins in Hvaler and Koster, my part of the project focused on the following questions:

1. How do the age structure and growth of sculpins vary between the two areas?
2. What is the parasite burden in the two areas?
3. Is there a covariance between the number of sealworms and weight of the sculpins?
4. How much do the number of sealworms per fish deviate from a random distribution (the Poisson distribution) in the two areas?

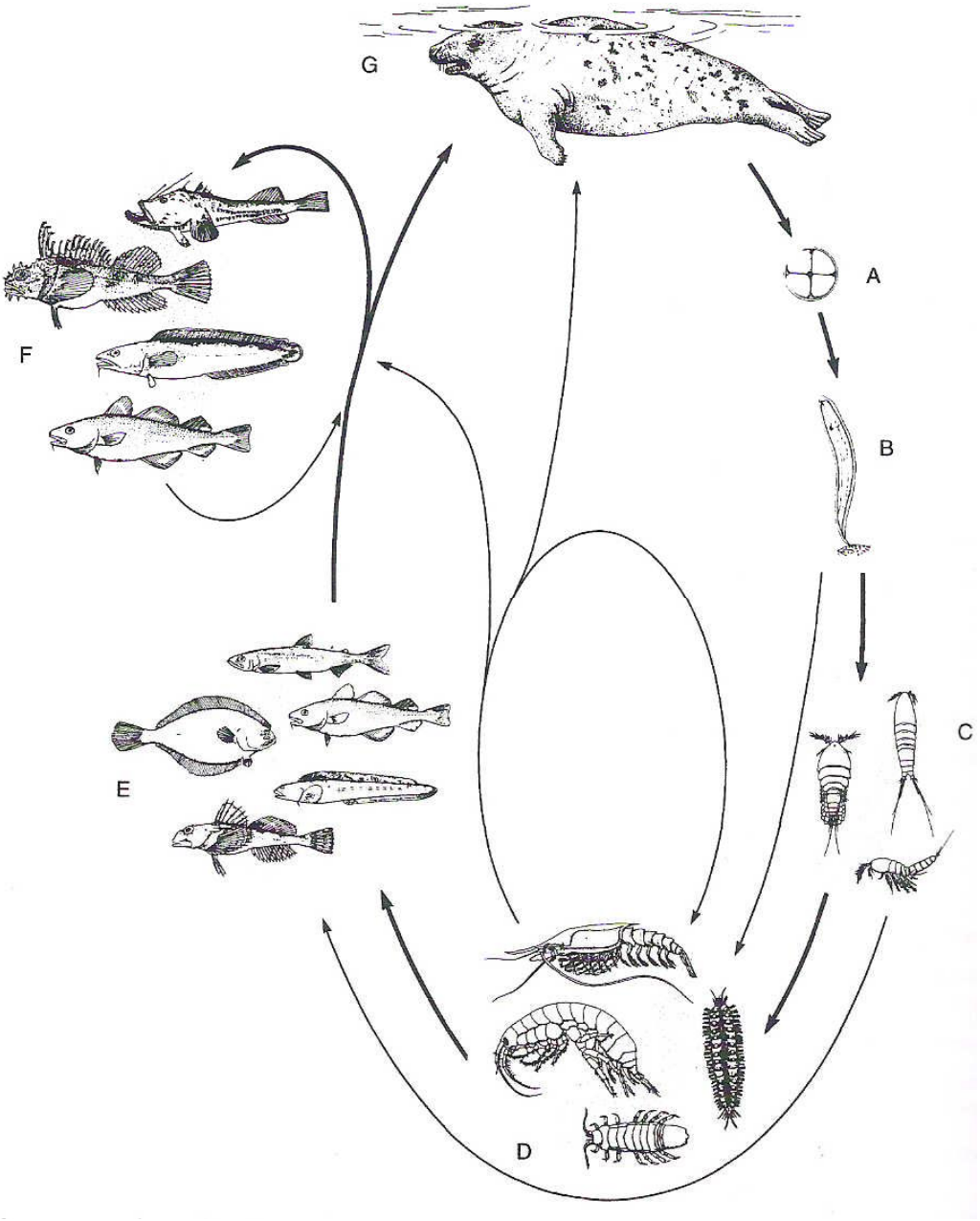

Figure 1.1. Life-cycle of *Pseudoterranova decipiens*. **A**. Eggs passed into the water with seal faeces. **B**. Second stage larvae adhered to substrate. **C** Second stage larvae in benthic harpacticoid and cyclopoid copepods. **D** Second stage larvae in macroinvertebrates (mysids, amphipods, isopods and polychaetes) **E**. Third stage larvae in musculature of benthophagous fish (juvenile cod, ocean pout, sculpins and plaice). **F** Third stage larvae in musculature of demersal piscivorous fish (cod, monkfish, sea raven). **G**. Fourth, fifth and adult stage in stomach of a seal (grey seal) (from McCelland et al. 1990).

1.1 Biology of the species

1.1.1 The sealworm (*Pseudoterranova decipiens*)

Sealworms (*Pseudoterranova decipiens*) are parasitic nematodes with seals as the main host (Figure 1.2). The life-cycle of sealworm incorporates several hosts and five developmental stages (Figure 1.1). The eggs are shed with seal faeces and sink to the bottom (McClelland 1990). The hatched larvae is ingested by the first intermediate host which is an isopode, a benthic harpacticoide or cyclopoide copepode, or a polychaete (McClelland 1990). Amphipods are claimed to be the important first intermediate host and a common prey item for heavily infected sculpins in the Oslofjord (Andersen 2001). There has been a general scientific consensus that the larvae occur in their second stage within invertebrates. However, it has recently been claimed that the larvae develops into the third stage (L3) within the egg (Køie et al. 1995; Berland 2003). In the first host the larvae grows from 0.25 mm to 0.50 mm in 1 to 5 weeks depending on temperature (McCelland et al. 1983; McClelland 1995). The larvae are then transmitted to a larger invertebrate host or to a fish host. Young fish get infected when feeding on benthic invertebrates. Cod fish, flatfish and sculpins are important intermediate hosts. When the invertebrate is eaten by a fish the yellow-brown *Pseudoterranova* larvae bore into the dorsal somatic muscle of the fish where it becomes encapsulated. The connective tissue of the capsule is produced by the fish and the *Pseudoterranova* larvae are there seen as light brown 'screws'. They grow to 30 – 40 mm and may live several years in the final host (McClelland 2002).

When the fish is eaten by a marine mammal or sea bird, the worm arrives in a warm stomach. If the host is correct, the larvae start to grow and develop into the adult stage. In the North Atlantic the definitive hosts are predominately grey seals, common seals and harp seals (McCelland et al. 1990). Grey seals are most heavily infected, followed by harbour seals. *P. decipiens* has also been found in walruses and bearded seals. First the larvae grow and moult to the 4th stage. The boring tooth is lost and lips develop. Finally they go through

the fourth moult and the last 5th stage appears. Now the reproductive organs develop and they become sexually mature.

Figure 1.2 A) Adult sealworms (*P. decipiens*) from the stomach of harbour seal from close to Finnøy. B) Third stage of *P.decipiens* from the fish host. Photo by Emma Lähdekorpi

1.1.2 Shorthorn sculpin (*Myoxocephalus scorpius*)

Shorthorn sculpin (*Myoxocephalus scorpius*), also called bullrout or short-spined sea scorpion, is mainly distributed in shallow coastal waters in the Northern Atlantic and adjacent subarctic waters (Moen & Svensen 2004). It is a small, long-living species which prefers shallow rocky-shores which are often near the seal skerries (Jensen & Andersen 1992). It is a very common species often seen from the shore to 30 m depths but also caught from the depths of 250 m (Moen & Svensen 2004). The larger specimens often lie on the sandy bottoms while the smaller individuals are found camouflaged amongst the kelp forest.

The sculpin has a characteristic flat head with a series of spines and bony plates (Figure 1.3). The coloration is variable from dark to greenish brown on the back with several dark spots and stripes on the sides. The belly is usually pale but during spawning the females

have orange belly and the males have reddish belly with white spots. The spawning time is in the winter months between December and March and age at maturity is 3 to 4 years (Pethon & Nyström 1998). The eggs are usually laid in the kelp bottoms, between algae and stones. One cluster can contain up to 2700 eggs. During the incubation period, which lasts for 1 – 3 months (depending on the temperature) males guard the roe. The larvae are pelagic for few months until they settle at the bottom at about 2 cm. Most of the adults are 20 – 30 cm; only a few large individuals are longer than 40 cm (largest species of the Cottidae). The diet consists of small fish, crustaceans and polychaetes (Jensen & Andersen 1992).

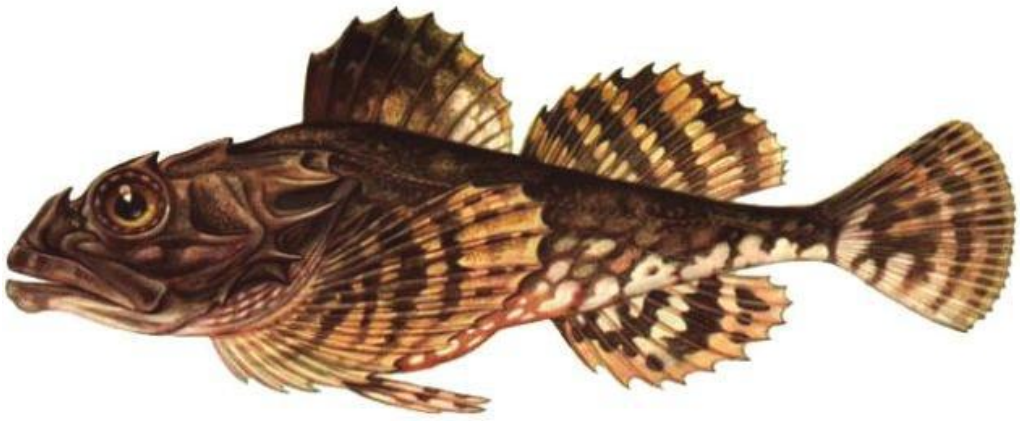

Figure 1.3 Shorthorn sculpin. Illustration from Svetocheva et al.(2007)

2 Materials and methods

2.1 Study area

Sealworm infection levels in sculpins were studied in two areas in outer Oslofjord: during September 2009 in the Hvaler area and in the autumn (mainly September –October) during the years 1991 - 1998 in the Koster archipelago about 15 km south from Torbjørnskjær (Figure 2.1). A small colony of 300 – 400 harbour seals inhabits the Torbjørnskjær skerries. When feeding, these seals disperse in the outer Oslofjord including the Hvaler Islands. During breeding, mating and moulting between May and October, the abundance of seals is greatest on the Torbjørnskjær skerries (Härkönen et al. 1999).

The Torbjørnskjær islands are located on the east side of the outer Oslofjord in southern Norway. The highly exposed Torbjørnskjær is based on a plateau which is about 2 km wide in south (Heia) and narrows to about 1 km in north (Torbjørnskjær Lighthouse) (Aspholm 1991). Most of the area is shallower than 20 m in depth and a series of trenches and depressions cut the plateau in various directions (Aspholm et al. 1995). The Torbjørnskjær archipelago is separated from the Hvaler Islands by a 10 km stretch of sea where the deepest parts exceed 250 m. The bottom consists of rock with small and large boulders in additions to some sandy bottoms in the south of the area (Heia) (Aspholm 1991).

The Hvaler islands consists of 4 large islands in a north-eastern direction (Kirkøy, Asmaløy, Spjærøy and Vesterøy) surrounded by many small islands and skerries. These islands are separated from the mainland by a inlet of about 4 km comprised of large areas with shallow depths of only 30 – 50 meters (Aspholm 1991). The sculpins for this study were caught near Asmaløy and Kirkøy approximately 10 km north-east from the seal haul-out skerries (Figure 2.1).

The Torbjørnskjær archipelago may be regarded as the northern part of the Koster archipelago in Sweden about 15 km south of the Heia in Hvaler (Figure 2.1). The Swedish part of this archipelago in northern Skagerrak consists of a huge number of skerries, islets

and islands with shallow areas in between, where the bottom is covered by sand, gravel or rocks (Lunneryd et al. 2001). There are four main areas where the seals are concentrated in the Koster islands and they prefer specific skerries for haul-outs (Figure 2.1). The fish were caught with 6 eel fyke-nets near the seal skerries (up to 300 m) close to Ursholmen and additional sampling was done 2 km southeast from Ursholmen.

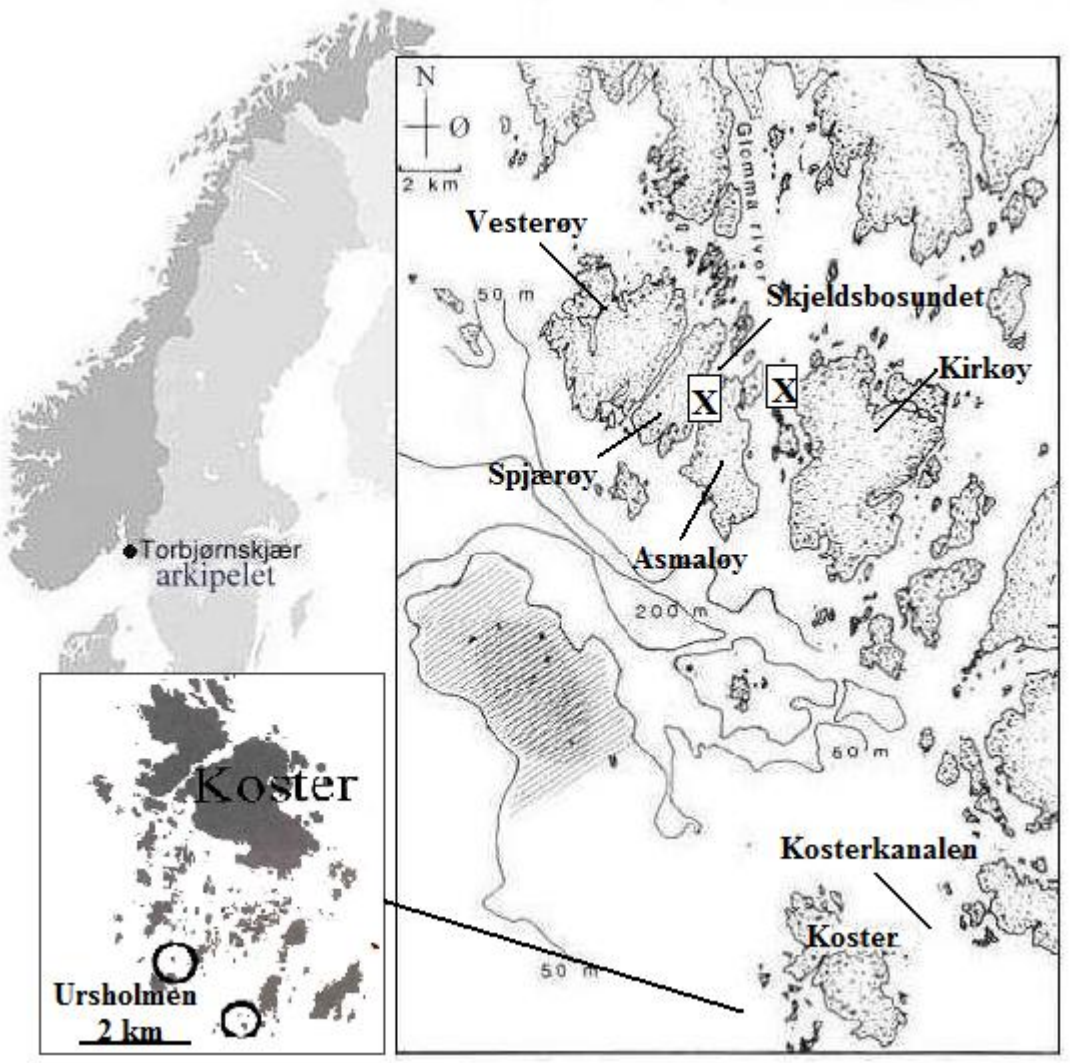

Figure 2.1 Locations where sculpins were collected at Asmaløy and Kirkøy in the Hvaler Islands (Norway) and Koster archipelago (Sweden). The hatched area and encircled skerries in Koster form the haul-out and whelping areas for the harbour seals (modified from Aspholm et al. 1995; Lunneryd et al. 2001; Damsgaard Jensen 2009).

2.2 Processing of the fish

All the fish caught were first frozen, then thawed in the laboratory and filleted before candling. The fork length (cm) of the fish was measured from the tip of the lower jaw to the edge of the caudal fin to the nearest 0.1 cm, and the weight (g) was measured to the nearest gram. The sex was observed from the gonads: females have larger gonads filled with roe in the spawning period. The otholits were removed for the age determination. Finally the fillets were placed on a light board in order to detect the parasites using the standard methods (Berland 1984).

2.2.1 Age determination

The white otoliths (ear-stones) are widely used for studying growth and age of fish and can also be used for species identification (Härkönen 1986; Brothers 1987; Mgaya 1995). In addition otoliths can be used to identify the prey species of marine mammals. Bony fishes have three pairs of otoliths, lapillus, asteriscus and sagitta, lying in three cranial cavities filled with endolymph in the skull (Figure 2.2) (Degens et al. 1969). All otoliths are composed of aragonite, which is a carbonate mineral and an organic compound of 0.2 to 10 %. The organic matter is a chemically relatively uniform protein which is similar in most fish groups. This fibrous protein resembles keratin in its amino acid composition. The mineralization of otoliths results in formation of calciumcarbonate-crystals. As the fish grows a series of concentric opaque and hyaline (translucent) zones are formed. Since the opaque zones are formed in summer and the hyaline zones in winter, the age of the fish may be determined by counting the number of zones (King 1983). The hyaline zone is relatively narrow because it is deposited in the winter when the growth is slower. The larger opaque zone is formed during late spring and summer when the growth is faster due to higher water temperature, primary production and abundant food sources (Mgaya 1995).

Sagitta is the largest of the ear-stones in marine fish and is therefore used for age determination (Härkönen 1986). The otoliths are placed on a Petri dish filled with 96 % rectified spirit for further examination under a microscope (King 1983). Sea scorpions have such small sagittas (Figure 2.2) that the growth zones may be counted in a stereo binocular after 6 – 10 minutes exposure with the spirits.

Sea scorpions have an extended spawning season (December – March), which can lead to a considerable variability in age and size within the same cohort (Jensen & Andersen 1992). Since our samples were taken mainly in September, we set the age to the number of growth zones plus 0.5 year. Thus the age was determined to 1.5, 2.5, 3.5 and 4.5 years.

Figure 2.2 Otoliths (Sagittae) of shorthorn sculpin from Hvaler. Photo by Emma Lähdekorpi

2.3 Detection and identification of the nematodes

The fish fillets were placed on a light board and illuminated from below in order to detect the parasites. All parasites were removed, stored in 70 % ethanol and identified according

to Berland (1961). The brownish nematodes encapsulated in the muscles were counted and identified as *Pseudoterranova decipiens*.

2.3.1 Characteristics of the sealworm – *Pseudoterranova decipiens*

The morphology and anatomy of the anisakid nematode *Pseudoterranova decipiens* are described in detail by Myers (2009) and Berland (1989). The larvae are yellowish-brown in color and are found most often in the dorsal part of the fish flesh where they are irregularly coiled. The tail of *P. decipiens* is characteristically short and sharply curved and has no spike comparable to *Anisakis simplex* (Figure 2.3 A). The head of *P. decipiens* is characterized by the very small boring tooth located on the same side as the excretory pore (Figure 2.3B).

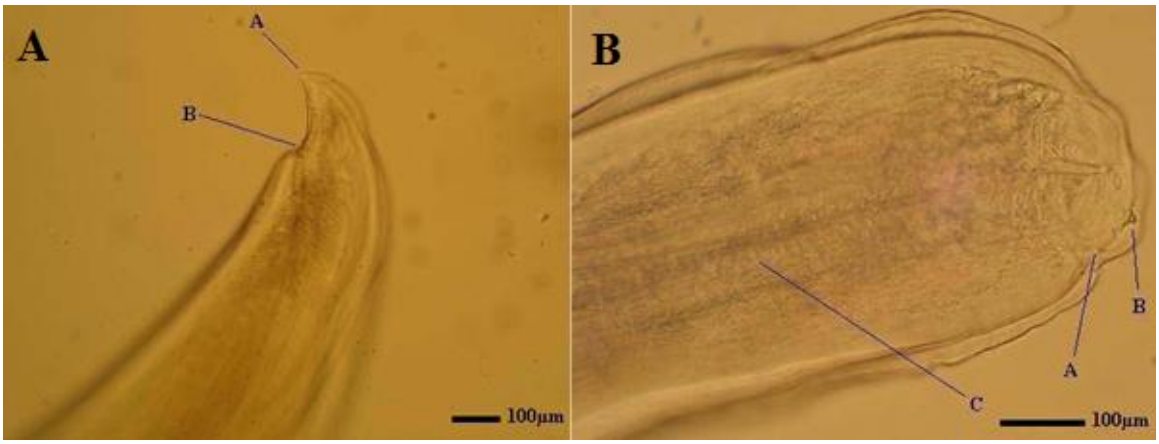

Figure 2.3 A) The curved tail of *P. decipiens* from anus (B) to the tip of the tail (A).
B) The head of *P.decipiens* with the boring tooth (B) esophagus (C) and the excretory pore (A). Photos by Martin Malmstrøm from Hansen and Malmstrøm (2006).

P. decipiens has a forward directed sac (intestinal caecum) in the anterior part of the intestine where the transverse transition between the intestine and esophagus is located (Figure 2.4). Intestinal caecum is characteristics for *P. decipiens* and can be used to distinguish it from *A. simplex*. Also the ventriculus is much smaller in *A. simplex* than in *P.*

decipiens. The cuticule is smooth and without prominent contours. Adult stages have well-developed bilobate lips with triangular oral cavity (Figure 2.4). The middle lips are missing. The shape and size of the lips are comparatively similar. The boring tooth is relatively small in *P. decipiens*.

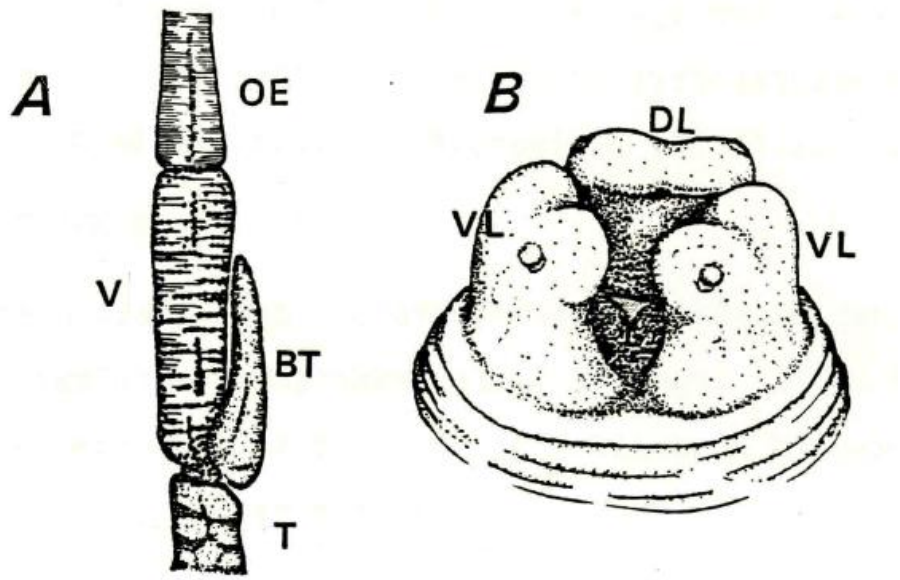

Figure 2.4 A) A part of the digestive canal of *Pseuoterranova decipiens*. OE = the posterior part of the esophagus. V = ventriculus BT = intestinal caecum that leads into the anterior part of the intestine (T). **B)** The oral parts seen from ventral-anterior direction. DL = dorsal lip. VL = ventrolateral lips. The triangular oral cavity is seen between the lips. Picture from Berland (1989).

A genetic study has revealed that there exist three sibling species of *Pseudoterranova decipiens* in the North Atlantic and Norwegian and Barents Sea (Paggi et al. 1991). Originally they were termed as *P. decipiens* A, B and C, but later named as *P. krabbei*, *P. decipiens* and *P. bulbosa* based on a genetic and morphological differences (Paggi et al. 2000). *P. krabbei* (*P. decipiens* A) appears to have distribution only in the North-East Atlantic, following primarily the distribution of grey seals (Paggi et al. 1991). However, some specimens have also been found from harbour seal. *P. decipiens* (B) is primarily a parasite of harbour seals but it also occurs in grey seals. In the northern North Atlantic

Ocean where the *P. krabbei* is not present, *P. decipiens* (B) is a parasite both of gray and harbour seals. *P. bulbosa* is found from the bearded seals at arctic waters. Since only harbour seals are found from outer Oslofjord and single grey seals are seen only sporadically during the summer (Aspholm et al. 1995), we assume that the specimens in our study are all type *P.decipiens* B.

2.4 Statistical methods

2.4.1 Infection rate

Margolis et al. (1982) recommended the following standard terminology for describing the infestation rate of sealworms. Prevalence is defined as the proportion of fish infested with sealworms (number of fish that contains at least one parasite divided by the total number of investigated fish). Abundance is defined as the average number of sealworms per investigated fish (i.e. total number of parasites divided by the total number of investigated fish). Intensity is defined as the average number of sealworms per infested fish (i.e. total number of parasites divided by the total number of investigated fish which had at least one parasite). These definitions also apply more specifically for the different sexes and age classes. Statistical tests (Chi-square test, Mann-Whitney) were run to check whether observed differences between sexes or age classes were significant. Finally a chi-square test was applied to test the fit of the Poisson distribution to the number of sealworms per fish.

2.4.2 Mortality rate

A rough estimate of the total instantaneous mortality rate, M, may be obtained from the slope of the catch curves were the logarithmic catch is plotted against the age (Quinn & Deriso 1999). Since shorthorn sculpin is not a target species for fisheries it may be assumed that the natural mortality is the same as the total mortality. This method assumes that there

is a constant recruitment and that each age group has the same catchability. Since the abundance of the year classes 2 – 4 were heavily dominating in the samples (more than 80 %), the instantaneous mortality was only calculated for these age groups. The annual natural mortality rate was then calculated as m = 1 – exp(-M):

Let N(t) denote the number of individuals at time t. If only natural mortality operates, the abundance follows the differential equation dN(t)/dt = -M*N Starting at age 2 the abundance at time t may therefore be given explicitly as N(t) = N(2)* exp(-Mt), from which it is seen that the instantaneous natural mortality (M), may be estimated as the coefficient in the linear regression of the logarithm of abundance against age:

Log(N(t)) = Log(N(2)) – M*t

Further, the relationship between two consecutive years is N(t+1) = N(t)*exp(-M). In other words, the annual reduction in abundance is

N(t) – N(t+1) = N(t) – N(t)*exp(-Mt) = N(t)*(1- exp(M))

We therefore obtain the annual natural mortality rate as m = [N(t) – N(t+1)]/N(t) = 1 – exp(-M)

2.4.3 Condition factor

The length and weight relationship, also known as condition factor, can be used to describe the well-being of fish (Williams 2000). The condition factor, K, is calculated by the equation (Ricker 1975) :

$K= 100\ W/L^3$, where W= total body weight (g), L= total length (cm)

The condition factor was used in order to compare the conditions of sculpins between Hvaler and Koster and to investigate if the sealworm burden had influence on the condition of sculpins

3 Results

In total 107 sculpins were sampled in the Hvaler Islands at Asmaløy and Kirkøy during September 2009 in a student project (Table 3.1; Appendix II). These fish were aged and investigated for presence of sealworm larvae in 2010. In addition we received the data from 161 sculpins sampled in the Koster archipelago during the 1990's in August – October (Table 3.1; Appendix III). This made it possible to compare the infections of nematodes in areas with very small (Hvaler) and very large (Koster) densities of harbour seals.

In both areas the sex ratio was skewed, but the percentage of females was very close to equal in the two very different systems: 69 % in Hvaler and 68 % in Koster (Table 3.1). While the females were between 1.5 and 4.5 years old, the males achieved one year less: 1.5 – 3.5 years (Figure 3.1 & 3.2). The length ranged between 12 and 29 cm among females and 12 and 21 cm among males (Appendix II & III).

Table 3.1 Mean age, length, weight, and number of sealworms in female and male shorthorn sculpins in Hvaler in 2009 and Koster in 1990's.

Area	Sex	n	%	Age	Lenght (cm)	Weight (g)	Pd
Hvaler	Females	74	69.2	3.4	20.2	150.3	0.5
	Males	33	30.8	2.6	16.7	67.8	0.3
Koster	Females	109	67.7	2.9	18.5	101.4	7.6
	Males	52	32.3	2.5	15.9	62.0	3.8

3.1 Age distribution

Females had a significant different age structure than males (Chi-square test, df = 3, $P \leq 0.001$; Appendix IV) and lived one year longer than the males (Figure 3.1 & 3.2). Roughly 80 % of the fish were between 2 and 4 year old in both areas. The fraction of 4.5 year old females was 26 % in Hvaler and 7 % in Koster. The fraction of 3.5 year old males

was 21 % in Hvaler and 19 % in Koster. While the age distribution of males was not significant different between the two areas (Chi-square test, df = 2, P = 0.81; Appendix IV), the females from Hvaler were significant older (Chi-square test, df = 3, P = 0.001; Appendix IV).

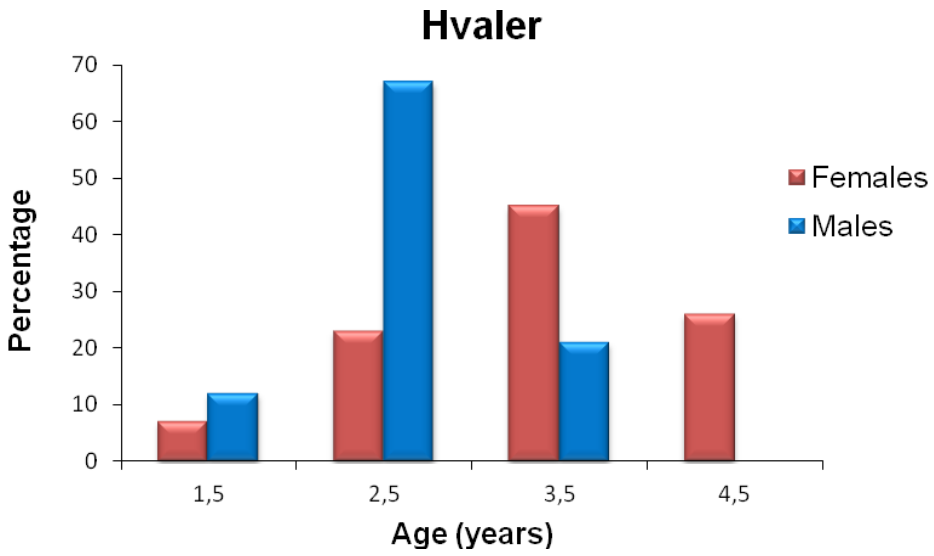

Figure 3.1 Age distribution of shorthorn sculpins in Hvaler.

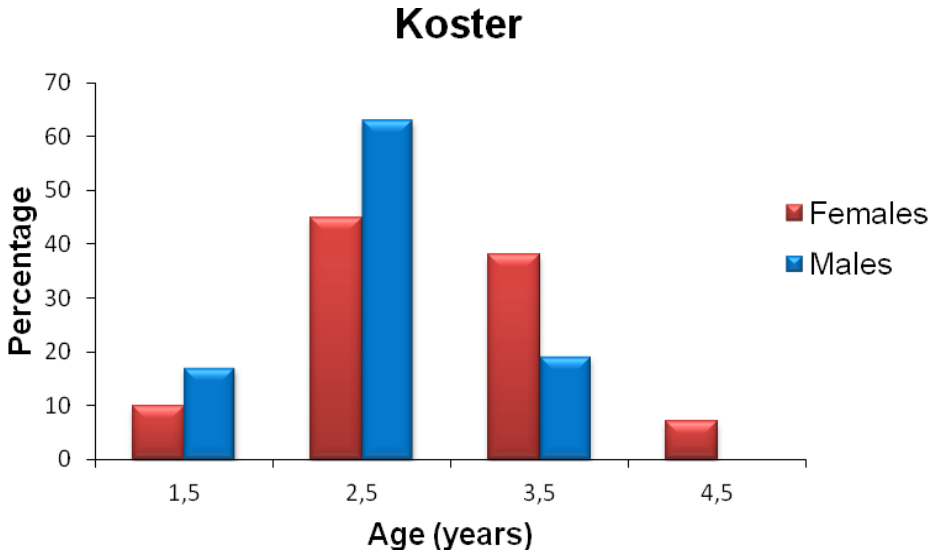

Figure 3.2 Age distribution of shorthorn sculpins in Koster.

3.2 Mortality rate

The total instantaneous mortality rate was 0.55 in females in Hvaler and 0.91 in Koster (Table 3.2; Figure 3.3 & 3.4). Males had two times higher mortality rates than females: 1.15 in Hvaler and 1.19 in Koster. The annual natural mortality rates were also higher in males: 0.68 in Hvaler and 0.70 in Koster, whereas 0.42 in females in Hvaler and 0.60 in Koster.

Table 3.2 Estimated mortality rates of shorthorn sculpin in Hvaler and Koster

		M	m
Hvaler			
	Females	**0.5521**	**0.42**
	Males	**1.1451**	**0.68**
Koster			
	Females	**0.9062**	**0.60**
	Males	**1.1939**	**0.70**

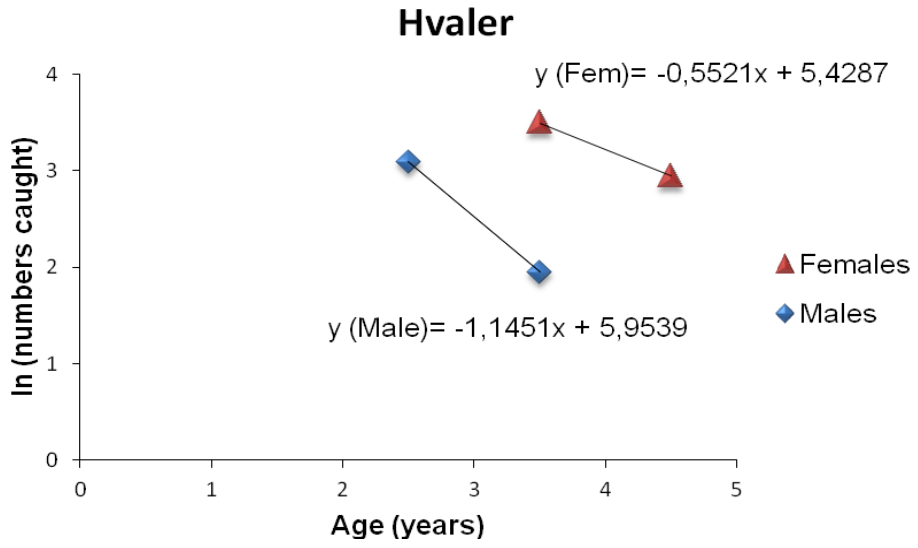

Figure 3.3 Total instantaneous mortality rates (M) of male and female shorthorn sculpins in Hvaler estimated from the linear regressions of ln(numbers caught) of each age group.

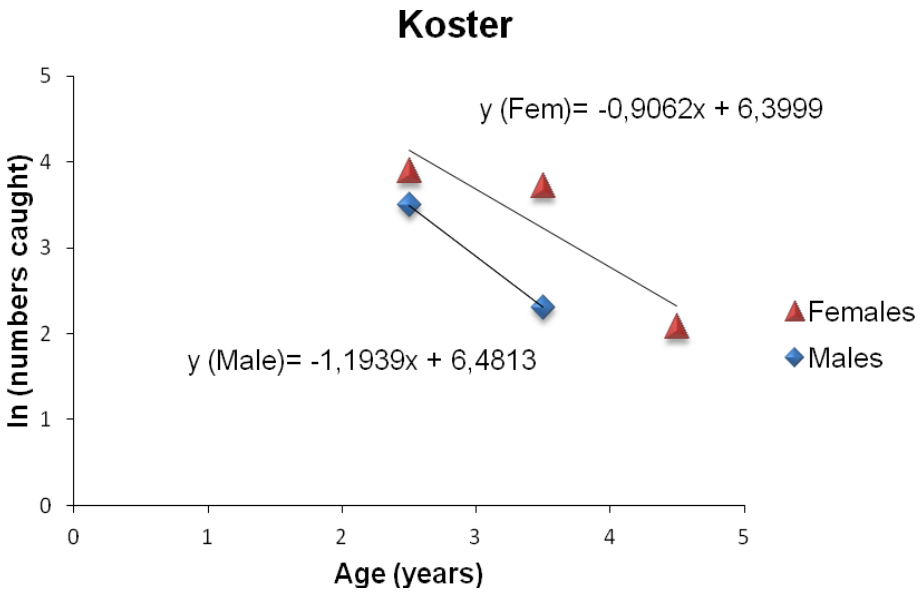

Figure 3.4 Total instantaneous mortality rates (M) of male and female shorthorn sculpins in Koster estimated from the linear regressions of ln(numbers caught) of each age group.

3.3 Length versus age

Figures 3.5 & 3.6 shows length plotted against age. On average, females became approximately 5 cm longer than males. In Hvaler an average female grew from about 13 cm at 1.5 years to about 24 cm at age 4.5, and an average male increased from 14 cm at age 1.5 to about 19 cm at age 3.5. In Koster an average female grew from about 14 cm at 1.5 years to about 24 cm at age 4.5, and an average male increased from about 13 cm at age 1.5 to about 19 cm at age 3.5. A linear growth model gave a significant approximation for both sexes in both areas ($P \leq 0.001$ in all cases; Appendix IV)

Hvaler	Females	Length (cm) = 7.27 + 3.80*Age
Hvaler	Males	Length (cm) = 10.20 + 2.50*Age
Koster	Females	Length (cm) = 8.56 + 3.39*Age
Koster	Males	Length (cm) = 9.33 + 2.61*Age

In Hvaler age explained 87 % of the variability in length for females and 78 % for males. In Koster the corresponding percentages were respectively 84 % for females and 78 % for males. During the first three years the sexes had approximately the same average length, until females become longer.

Females had practically identical length growth in Hvaler and Koster (Figure 3.7). Males from Hvaler were significant longer than males in Koster (Figure 3.7; Linear regression, df = 82, P = 0.002; Appendix IV). However this difference in length was only about 0.5 cm and therefore of no ecological significance.

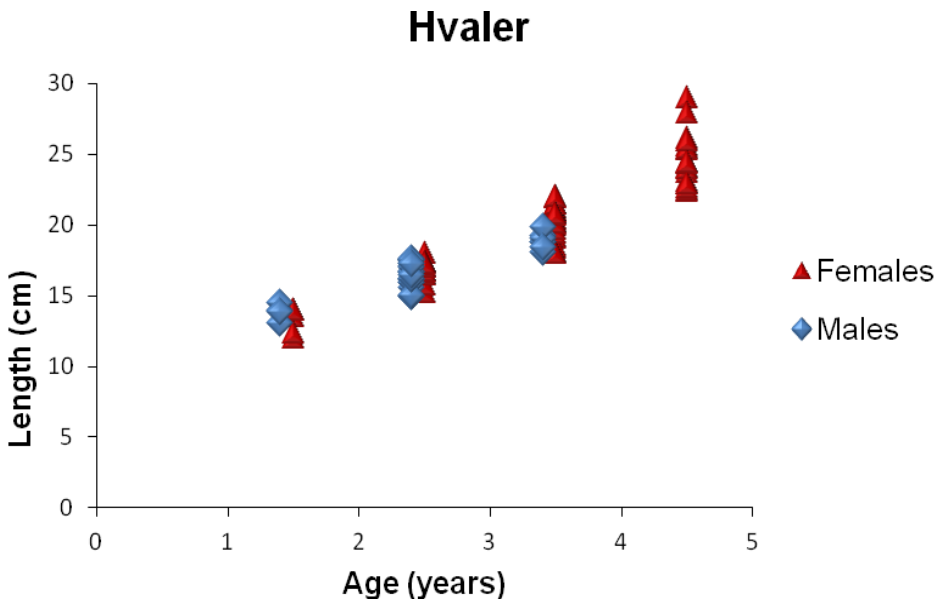

Figure 3.5. Length versus age for sculpins in Hvaler.

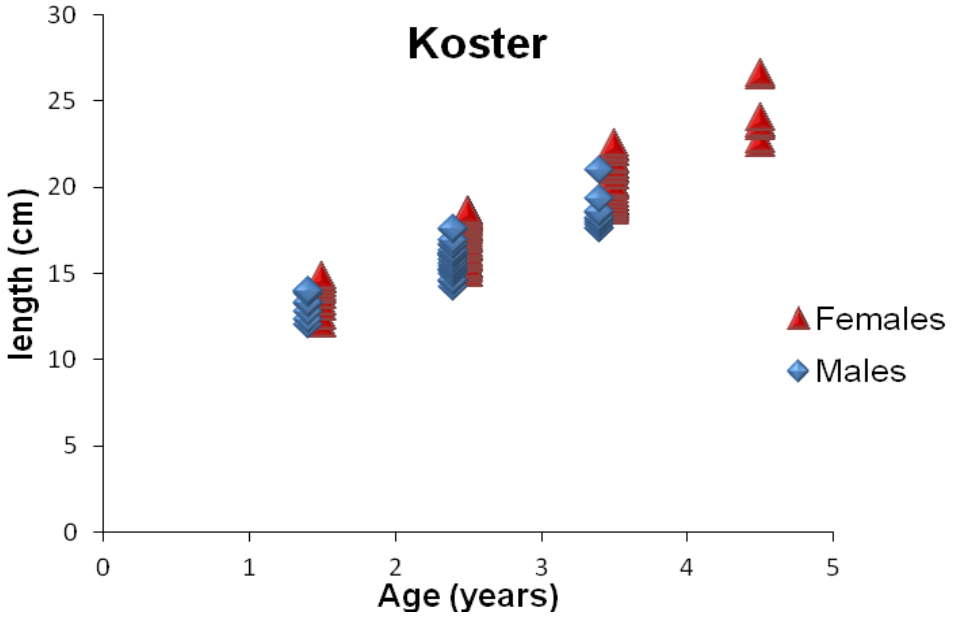

Figure 3.6. Length versus age for sculpins in Koster.

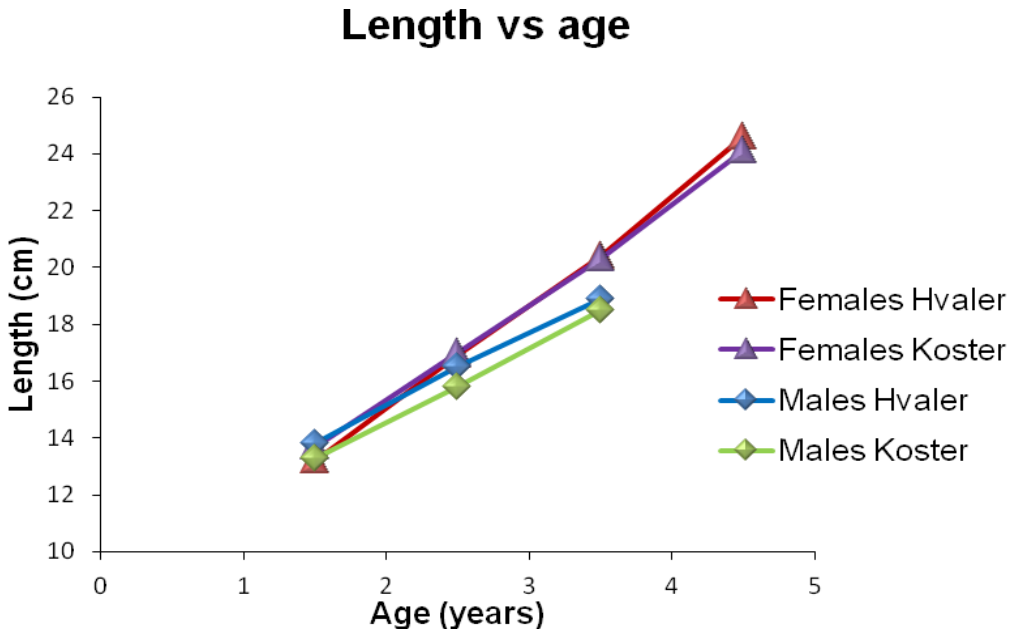

Figure 3.7 Length versus age for female and male sculpins in Koster and Hvaler.

3.4 Weight versus age

Figures 3.8 & 3.9 shows weight plotted against age. Females became significantly larger than males. In Hvaler an average female grew from about 35 g at 1.5 years to about 265 g at age 4.5, and an average male increased from the same size at age 1.5 to about 105 g at age 3.5. In Koster an average female grew from about 35 g at 1.5 years to about 210 g at age 4.5, and an average male increased from about 25 g at age 1.5 to about 100 g at age 3.5. A polynomial growth model gave a significant approximation, but the sexes had significant different degrees (Appendix IV). While females required a quadratic model, males could be approximated by a linear model:

Hvaler	Females	Weight (g) = 64.4 – 51.4*Age + 21.2 Age*Age
Hvaler	Males	Weight (g) = -21.0 + 35.7*Age
Koster	Females	Weight (g) = 15.5 – 2.7*Age + 10.3 Age*Age
Koster	Males	Weight (g) = -28.4 + 35.9*Age

In Hvaler age explained 77 % of the variability in weight for females (quadratic model) and 80 % for males (linear model) (Appendix IV). In Koster the corresponding percentages were respectively 78 % for females (quadratic model) and 68 % for males (linear model) (Appendix IV). During the first two years the sexes had approximately the same average weight. At age 3 females start to become larger. This is reflected in the fitted growth curves (Figure 3.8 & 3.9). Only for females does the quadratic growth curve give a significant improvement compared to a linear model ($P \leq 0.001$ for females in both areas and $P \geq 0.33$ for males in both areas; Appendix IV).

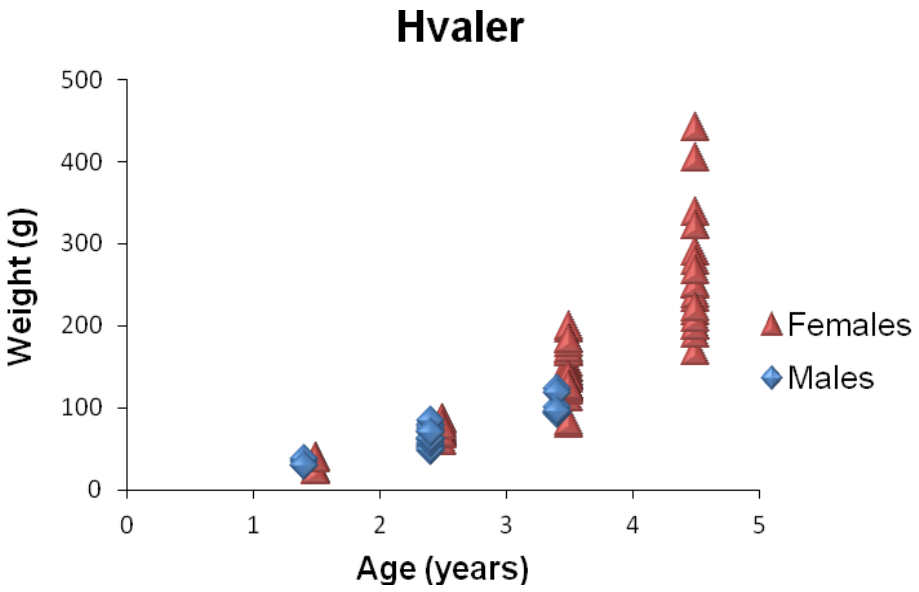

Figure 3.8 Weight versus age for sculpins in Hvaler.

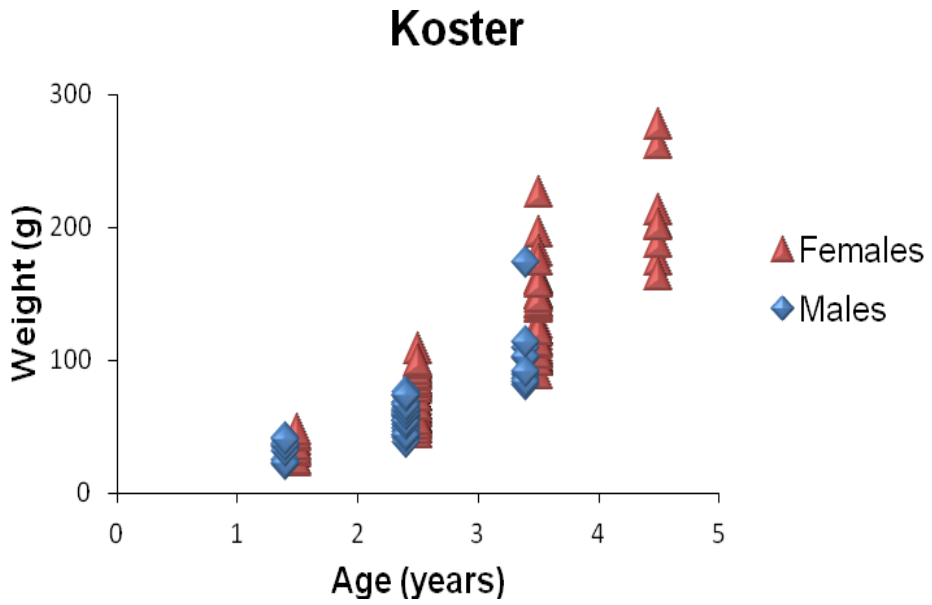

Figure 3.9 Weight versus age for sculpins in Koster

Both females and males seemed to have a different growth in Hvaler and Koster (Figure 3.10). Females followed approximately the same growth up to age 3 but obtained larger weights in Hvaler. The observed average weights for 4 year old females were 265 g in Hvaler (n = 19) and 211 g in Koster (n = 8). However, due to a large variability (a combined standard deviation SD = 65.6 g), this difference is not significant (t-test, df = 25 & P = 0.062; Appendix IV). It is further seen that the males have the same growth rate of 36 g/year, but males from Hvaler are approximately 6 g heavier. However, again due to a high variability, this difference is not significant (P = 0.29; Appendix IV).

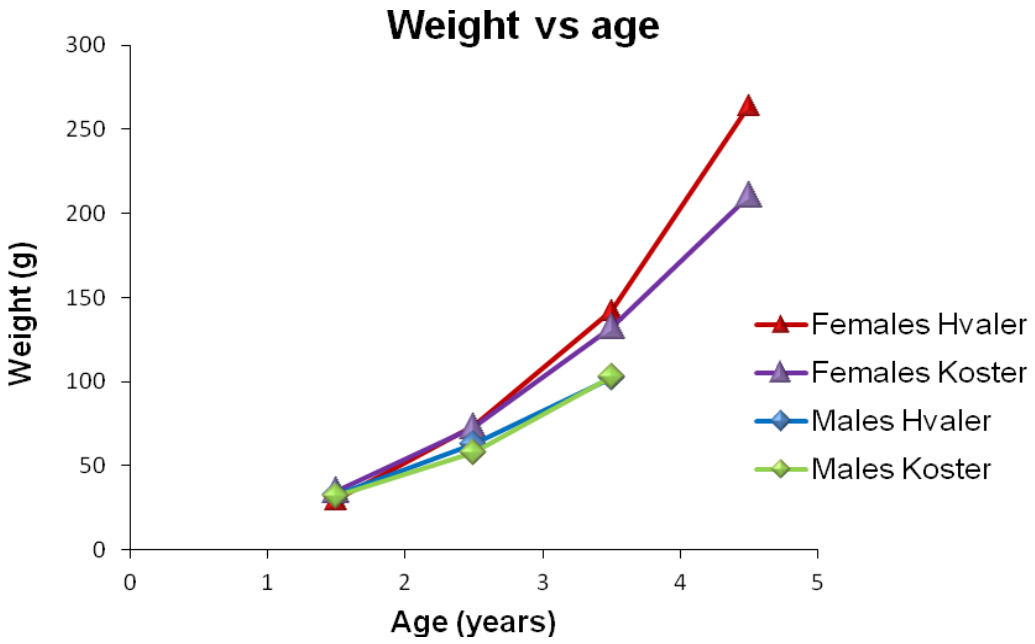

Figure 3.10 Weight versus age for female and male sculpins in Hvaler and Koster.

3.5 Condition factor

The relationship between condition and age of female and male sculpins in Hvaler and Koster are shown in figures 3.11 and 3.12. The condition increased slightly with increasing age until the age of 3.5 in both sexes in Hvaler and Koster (Table 3.3). In Hvaler the

condition decreased in 4.5 years old females. Age explained 24 % of the variation in condition in females and 30 % in males in Hvaler. In Koster age explained only 9 % of the variation in condition in females and 23 % in males. The females had better average condition (1.63, SD = 0.24) than males (1.41, SD = 0.14) in Hvaler while in Koster the both sexes had the same condition (females: 1.45, SD = 0.18, males: 1.46, SD = 0.16; Table 3.3).

Table 3.3 Estimated condition factors (K) for different age groups of female and male sculpins in Hvaler and Koster.

	Hvaler		Koster	
age	Females	Males	Females	Males
1.5	1.3	1.4	1.3	1.3
2.5	1.4	1.4	1.5	1.4
3.5	1.6	1.6	1.7	1.5
4.5	1.5		1.7	
avg	1.45	1.46	1.63	1.41
SD	0.18	0.16	0.24	0.14

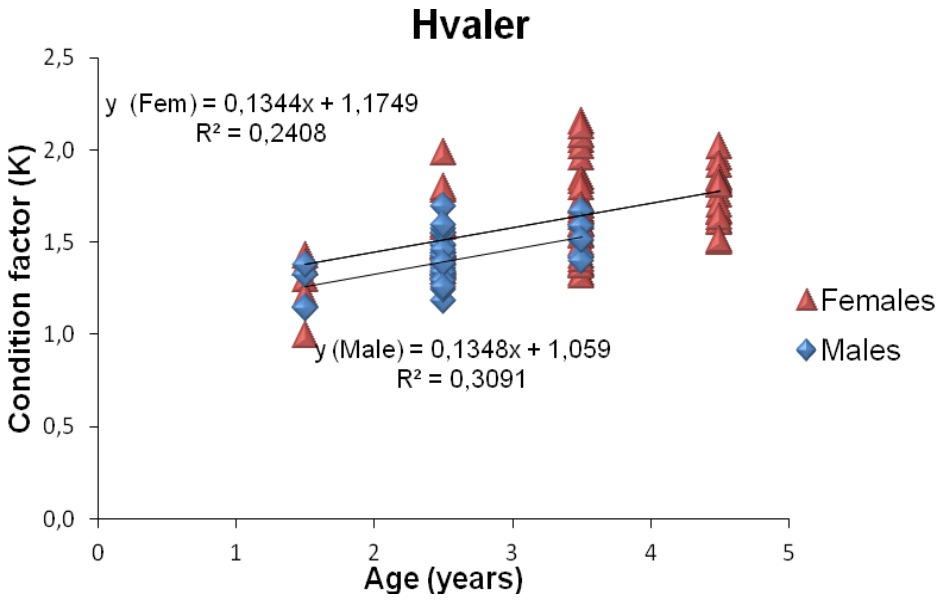

Figure 3.11 Relationship between condition and age for female and male sculpins in Hvaler

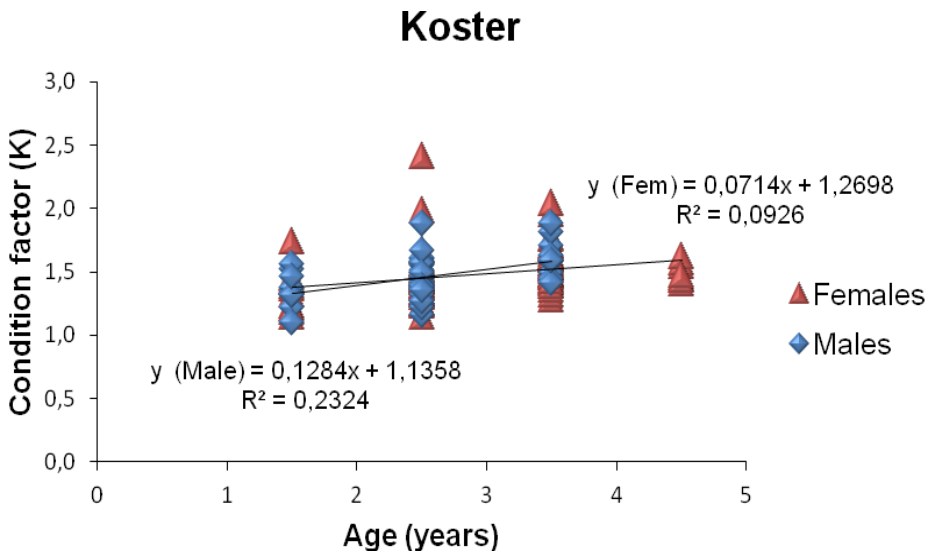

Figure 3.12 Relationship between condition and age for female and male sculpins in Koster.

3.6 Infestation rate of sealworms

In Hvaler 27 % of the females and 18 % of the males were infested by sealworms (Table 3.4 & 3.5) and the number of sealworm per fish varied between 0 and 4 (Appendix II). On average, the abundance (total number of sealworms divided by total number of investigated fish) was 0.4 for females and 0.3 for males in Hvaler, while the intensity (total number of sealworms divided by total number of infested fish) was 1.7 for females and 1.5 for males (Table 3.4 & 3.5). The difference between the sexes in prevalence (fraction infested) was not significant in Hvaler (Chi-square test for prevalence; df = 1, P = 0.32; Appendix IV).

In Koster 87 % of the females and 79 % of the males were infested by sealworms (Table 3.6 & 3.7) and the number of sealworm per fish varied between 0 and 34 for females with the exception of 102 sealworms in one female (Appendix III). In males the range was 0 - 14. On average, the abundance was 7.6 for females and 3.8 for males in Hvaler, while the intensity was 8.7 for females and 4.8 for males (Table 3.6 & 3.7). The difference between

the sexes in prevalence (fraction infested), abundance and intensity was not significant in Koster (Chi-square test for prevalence; df = 1, P = 0.17; Mann-Whitney for abundance and intensity, P = 0.44 – 0.46; Appendix IV).

Table 3.4 Infection statistics of *P.decipiens* in female sculpin in Hvaler.

Age	Prevalence	Abundance	Intensity
1.5	20	0.4	2.0
2.5	35	0.4	1.0
3.5	24	0.5	2.0
4.5	26	0.5	1.8
ALL	27	0.4	1.7

Table 3.5 Infection statistics of *P.decipiens* in male sculpin in Hvaler.

Age	Prevalence	Abundance	Intensity
1.5	0	0.0	0.0
2.5	18	0.3	1.8
3.5	29	0.3	1.0
ALL	18	0.3	1.5

Table 3.6 Infection statistics of *P.decipiens* in female sculpin in Koster.

Age	Prevalence	Abundance	Intensity
1.5	82	3.5	4.3
2.5	82	4.2	5.2
3.5	93	11.5	12.4
4.5	100	13.6	13.6
ALL	87	7.6	8.7

Table 3.7 Infection statistics of *P.decipiens* in male sculpin in Koster.

Age	Prevalence	Abundance	Intensity
1.5	67	2.4	3.7
2.5	79	3.2	4.0
3.5	90	7.0	7.8
ALL	79	3.8	4.8

Table 3.8 Mean infection levels of *P.decipiens* in sculpins from Hvaler and Koster.

	Prevalence	Abundance	Intensity
Hvaler	24	0.4	1.6
Koster	85	6.4	7.5

There was almost no correlation between the number of sealworm and weight of the fish (Figure 3.13, 3.14 & 3.16). There was a small correlation with weight and number of sealworms in female sculpins in Koster (Figure 3.15). Although, weight explained only 17 % of the variation in sealworm numbers in female sculpins in Koster.

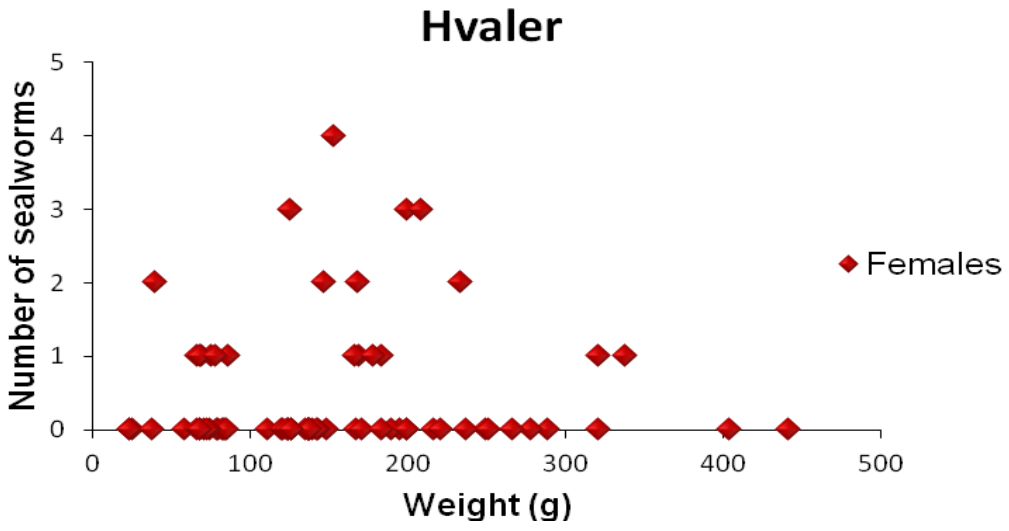

Figure 3.13 Number of sealworms (*Pseudoterranova decipiens*) versus weight for female sculpin in Hvaler

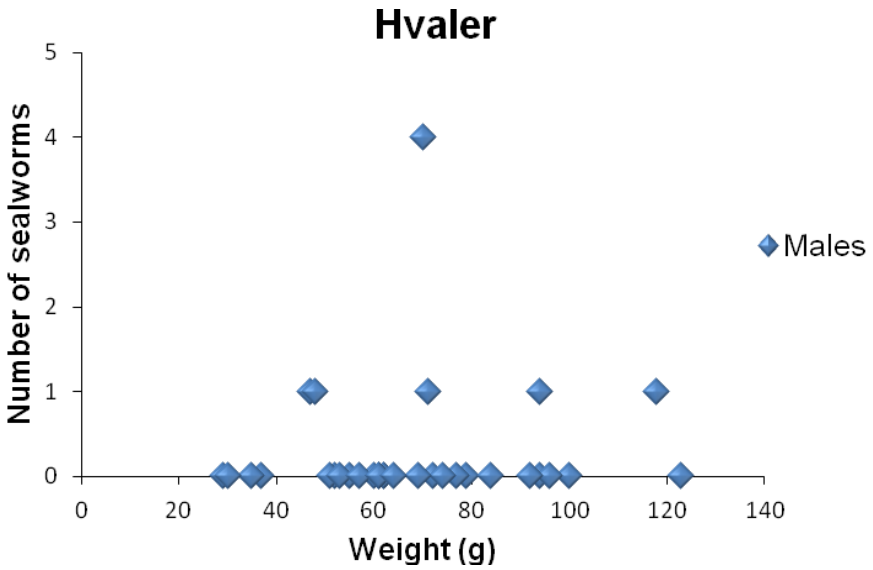

Figure 3.14 Number of sealworms (*Pseudoterranova decipiens*) versus weight for male sculpin in Hvaler.

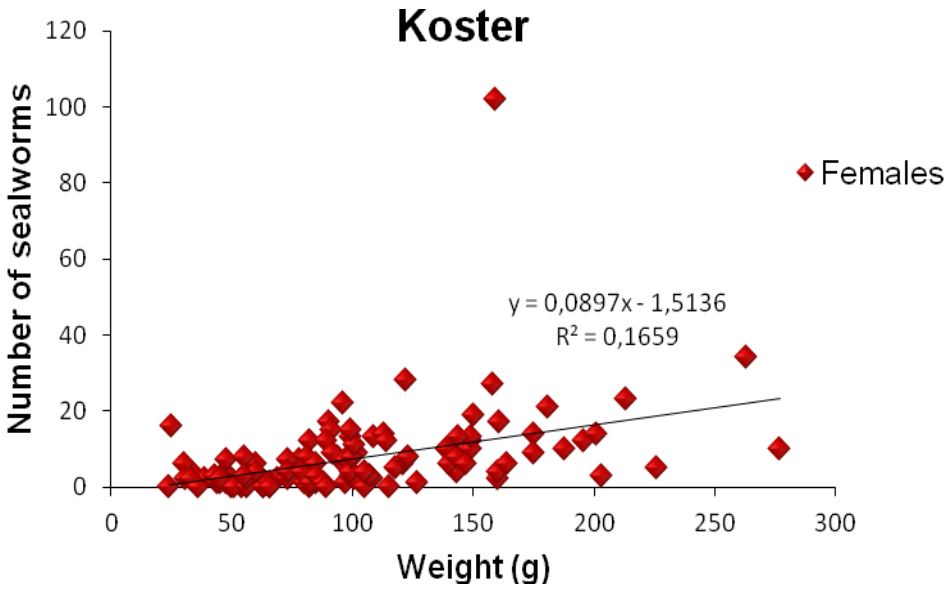

Figure 3.15 Number of sealworms (*Pseudoterranova decipiens*) versus weight for female sculpin in Koster.

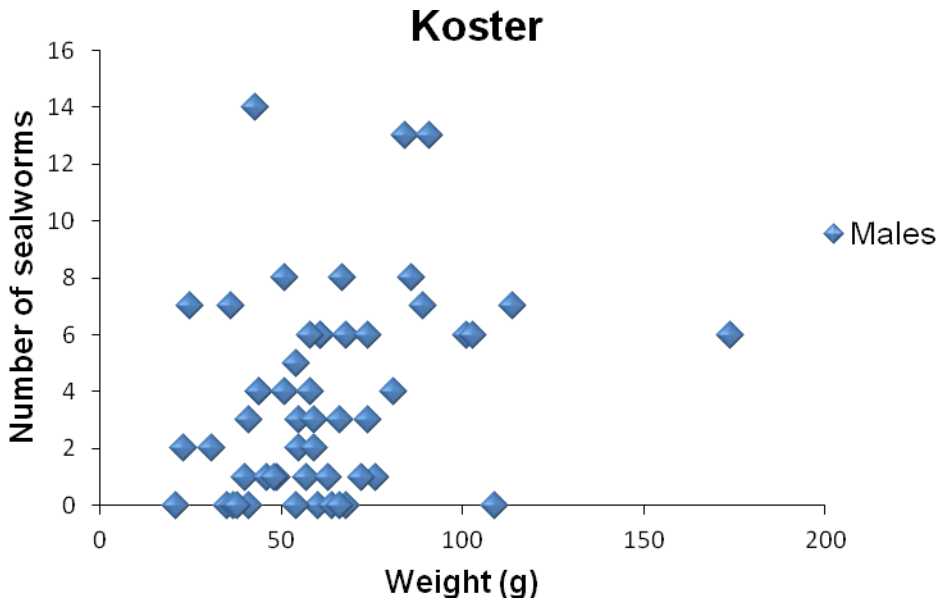

Figure 3.16 Number of sealworms (*Pseudoterranova decipiens*) versus weight for male sculpin in Koster.

3.8 Distribution of number of sealworms per fish

The number of fish infested with a given number of sealworms is shown in figures 3.17 – 3.22 for both sexes in both areas. It is seen that the number of sealworms per fish follows a Poisson distribution in Hvaler, and has a large deviation from the Poisson distribution in Koster.

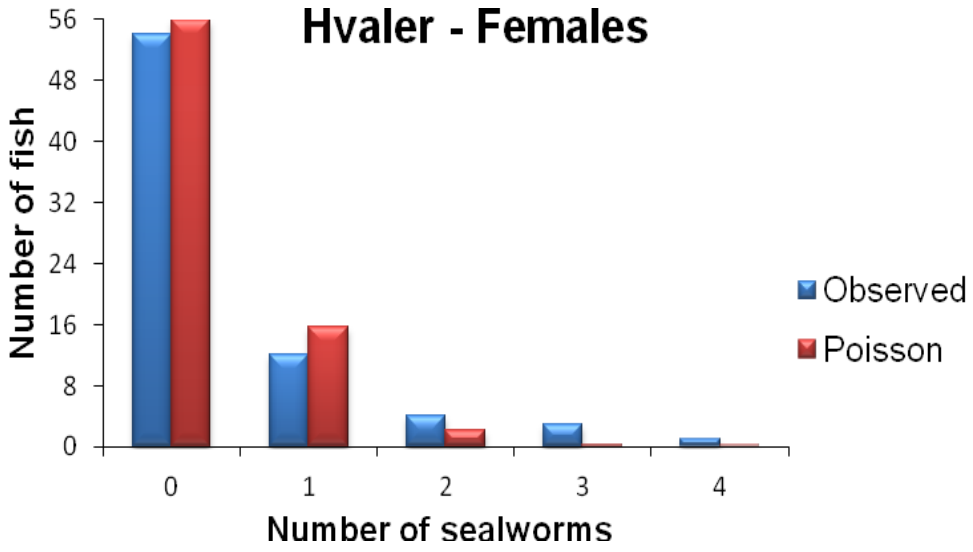

Figure 3.17 Observed histogram of the number of sealworms (*Pseudoterranova decipiens*) per female sculpins from Hvaler, and fitted Poisson distribution with parameter $\lambda = 0.28$.

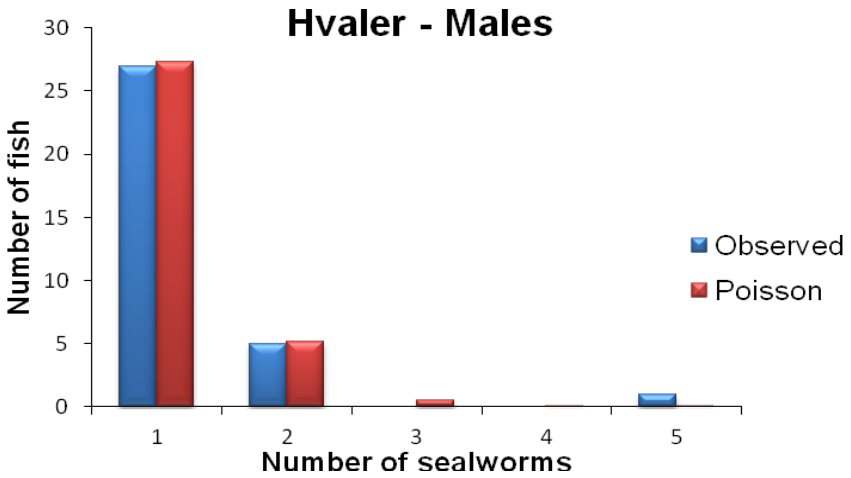

Figure 3.18 Observed histogram of the number of sealworms (*Pseudoterranova decipiens*) per male sculpins from Hvaler, and fitted Poisson distribution with parameter $\lambda = 0.28$.

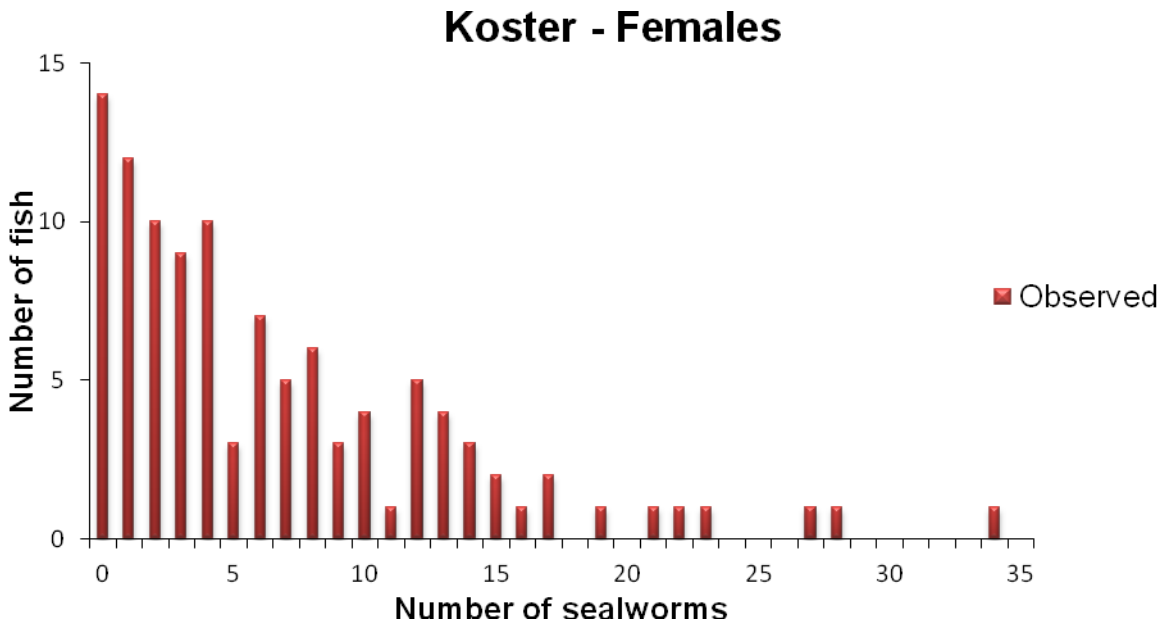

Figure 3.19 Observed histogram of the number of sealworms (*Pseudoterranova decipiens*) per female sculpins from Koster. One female with 102 sealworms was excluded.

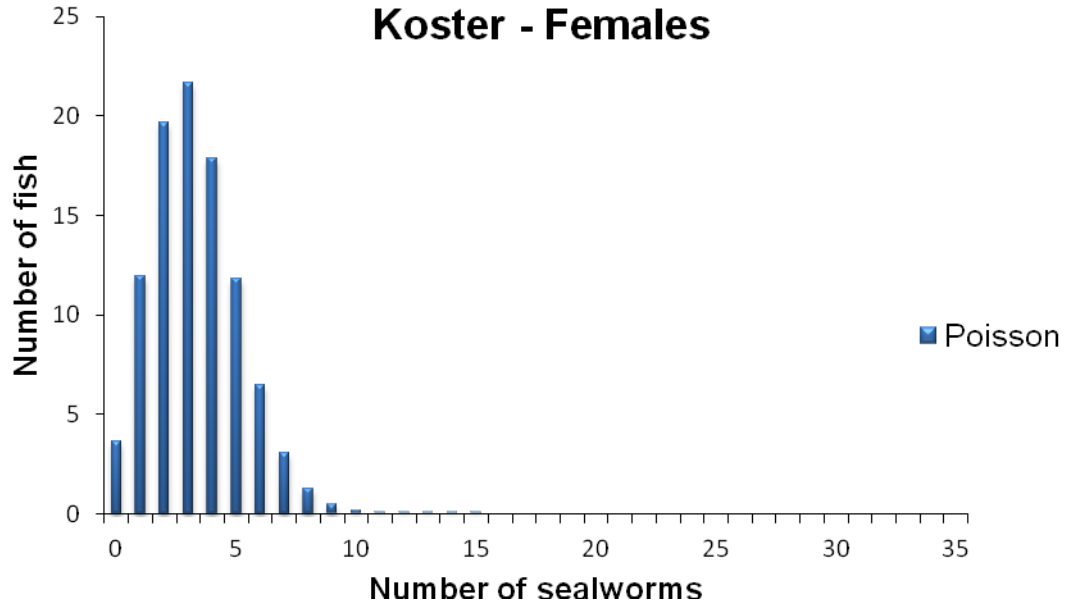

Figure 3.20 The best approximation with the Poisson distribution (parameter $\lambda = 3.19$) to the observed histogram of the number of sealworms (*Pseudoterranova decipiens*) per female sculpins from Koster. The fitted Poisson distribution is significantly different (Chi Square Test; $P < 0.001$) from the observed histogram.

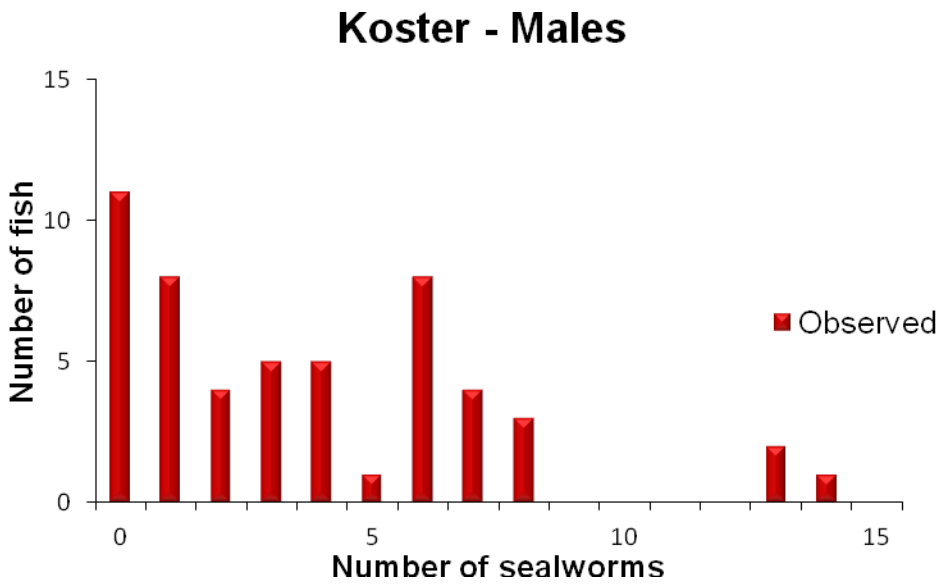

Figure 3.21 Observed histogram of the number of sealworms (*Pseudoterranova decipiens*) per male sculpins from Koster.

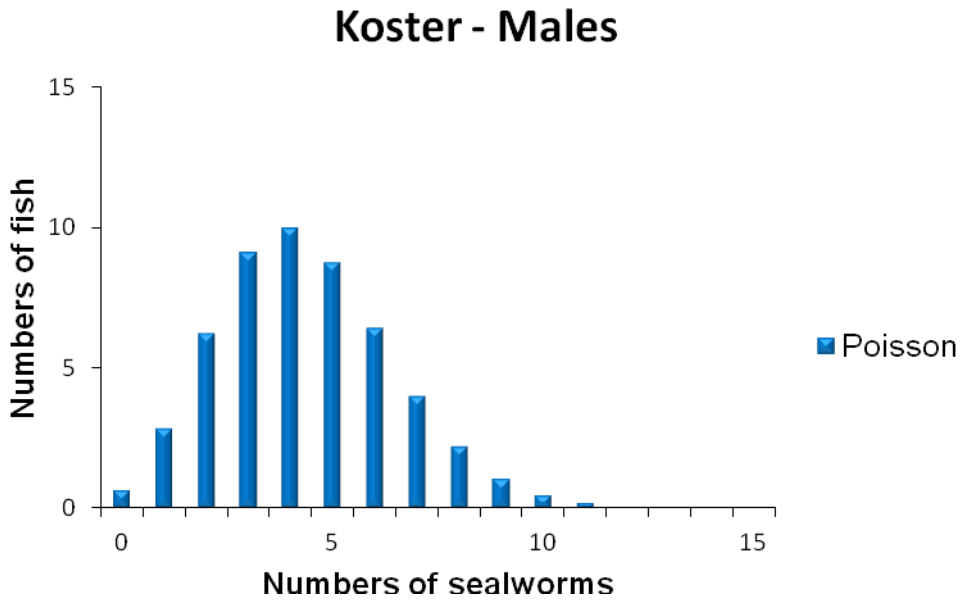

Figure 3.22 The best approximation with the Poisson distribution (parameter $\lambda = 4.38$) to the observed histogram of the number of sealworms (*Pseudoterranova decipiens*) per male sculpins from Koster. The fitted Poisson distribution is significantly different (Chi Square Test; $P < 0.001$) from the observed histogram.

4 Discussion

A heavy burden of sealworms (*Pseudoterranova decipiens)* in shorthorn sculpin (*Myoxocephalus scorpius*) in the North Atlantic waters, indicates an important role of intermediate host and transmitter to seals or other fish species (Háuksson 1989; Jensen & Andersen 1992; Kerstan 1992; Aspholm et al. 1995; Jensen 1997a). A large colony of harbour seals supports large populations of sealworms in sculpins in the Koster archipelago. In contrast, a small number of harbour seals visiting in the Hvaler islands results in a low abundance of sealworms in sculpins. It is also documented that there is a complex relationship between the abundance of sealworms in fish and seals (Jensen et al. 1994a; Langvald 2000; Andersen 2001; Marcogliese 2001). In addition age, size and diet of the intermediate host may influence the number of sealworms in fish (des Clers 1989; Jensen et al. 1994b).

4.1 Methods

When analyzing the results, some considerations should be taken into account. Sculpins were caught with fyke-nets and therefore had to swim in order to be caught in the net. However, fishes of different age or size may have different activity levels (Luksenburg & Pedersen 2002) and therefore induce a bias in the observed age- and size distributions and the estimated mortality rates.

The locations of the sampling stations in Hvaler and Koster were not similar in relation to the proximity of the haul-out places of the seals. In Koster the sculpins were caught near the seal skerries (max. 300 m from the skerries), while in Hvaler the sampling stations were 10 km north-east of the seal skerries (Figure 2.1). Because sealworm infection level decreases with increasing distance from the skerries (Jensen & Idås 1992), the sculpins taken far from the skerries have smaller infection levels than sculpins near the skerries. This could explain the different infection levels observed in Hvaler and Koster (Table 3.4 –

3.7). However, harbour seals have been observed swimming in the Inner Hvaler area were the sculpins were caught (Langvald 2000).

The sample size of 161 sculpins from Koster is small in relation to the long sampling period from 1991 to 1998, so a fluctuation in recruitment may induce a bias in the observed age- and size structure (Table 3.1). The estimated annual mortality rates must therefore only be considered as average levels during the investigated periods (Table 3.2).

The samplings were conducted in Koster in the 1990's and in 2009 in Hvaler. Over ten years the growth rate may change due to different environmental conditions (Wootton 1998). Therefore the differences in the condition factor may be due to time rather than habitat (Table 3.3).

4.2 Age structure

Although the shorthorn sculpin is a long-lived species (Pethon & Nyström 1998), the age structure differs significantly between populations. In Hvaler and Koster the female sculpins had significantly different age structure than males (Chi-square test, df = 3, $P \leq 0.001$; Appendix IV) and lived one year longer (Figure 3.1 & 3.2). According to several studies, there are significant differences between the sexes within the same population in growth, mortality, length at maturity and longevity (Lamp 1966; Ennis 1970a; Ennis 1970b; King 1983; Raciborski 1984; Luksenburg & Pedersen 2002). For example, female sculpins in Tromsø grew larger, matured at larger sizes, lived one year longer and had lower mortality rates compared to males. Maximum age was estimated to be 6 years for females and 5 years for males, but most of the females were between 1 – 3 years and males 1 – 2 years, which is close to the values observed in our study (80 % between 2 – 4 years; Figure 3.1 & 3.2). Fish populations in the northern and colder part of the species range are often long-lived (Beverton 1992), although shorthorn sculpins in northern Norway are more similar to short-lived central European populations (Luksenburg & Pedersen 2002).

In the central European waters sculpins do not usually exceed the age of 6 years (Luksenburg & Pedersen 2002), while on the other side of Atlantic in Newfoundland, sculpins have been observed to live up to 14 (males) and 15 (females) years old (Ennis 1970b). In contrast the maximum age recorded in Galway Bay, Ireland, was only 3 years for both sexes (King 1983). In our study the oldest females were 4.5 years and oldest males 3.5 years (Figure 3.1 & 3.2). In a comparable study from Torbjørnskjær, the oldest sculpins were 10 years (Jensen et al. 1994b). However, the mean age of the population (4.1 years) was only approximately one year more than in our study (3.0 years in Hvaler, 2.7 years in Koster; Table 3.1). In addition, Andersen (2001) recorded a high maximum age of sculpin (10 years) in Hvaler, whereas most of the sculpins ranged between 3 – 5 years. Probably with a bigger sample size and more comprehensive data we would also got some representatives from the older age classes.

Comparable age structures of sculpins was reported in a study by Langvald (2000) in Hvaler and Koster. There was higher proportion of older females than males: 37 % of the females in Hvaler and 40 % in Koster were over 3 years old, whereas only 12 % of the males in Hvaler and 21 % in Koster were older than 3 years. We found similar numbers of over 3 years old sculpins in Koster (45 % of females and 19 % males; Figure 3.2). In Hvaler the proportion of older individuals had almost doubled in ten years (71 % of females over 3.5 years; 21 % of the males over 3.5 years; Figure 3.1). The change in age structure towards older population indicates increased survival rates.

The age structure in Koster was also similar to what was found in a population of mosshead sculpin (*Clinocottus Globiceps*, Girard 1857) in tide pools in Helby Island, Canada (Mgaya 1995). 77.2 % of the specimens were from 1 to 3 years old and only 9 % was older than 4 years (In Koster 63 % were 1-3 years and 7 % over 4.5 years; Figure 3.2). Sculpins living in tide pools are exposed to high environmental variation and harsh conditions. Similar age structure found in a species from the same sculpin family in an exposed habitat indicates that the sculpin population in Koster also experiences a high natural mortality.

Female sculpins in Hvaler were significant older than in Koster (Chi-square test, df = 3, P = 0.001; Appendix IV). The fraction of oldest year class 4.5 was 26 % in Hvaler and 7 % in Koster (Figure 3.1 & 3.2). 71 % of the females were over 3.5 years in Hvaler, while in Koster most of the females were under 3.5 years (55 %). Females were observed to live longer in Hvaler than in Koster, which can be due to higher natural mortality rate of females in Koster. The instantaneous mortality rates (M) were 0.55 in Hvaler and 0.90 in Koster (Table 3.2). Koster sculpins have much higher sealworm infection rates than sculpins in Hvaler (Table 3.4 – 3.7), and that can lead to lower condition of the older sculpins and make them more prone to predation. This is supported by the higher conditions rates (K) found in 4.5 year old female sculpins in Hvaler (K = 1.74) than in Koster (K = 1.49; Table 3.3). High sealworm infections may also reduce the swimming speed of fish (Sprengel & Luchtenberg 1991). The age distribution of males as well as the mortality rates and condition factors were fairly similar between the two areas.

The finding that female sculpins lived longer and also grew faster (females became approximately 5 cm longer than males; Figure 3.7) in both areas indicates that males have higher natural mortality rate. This is supported by the rough mortality rates estimated in our samples (Table 3.2). The males have twice as high total instantaneous mortality rate (M) (M = 1.15 in Hvaler and M = 1.19 in Koster) than females (M = 0.55 in Hvaler and M = 0.91 in Koster). The annual natural mortality (m) is also slightly higher in males (m = 0.68 in Hvaler; m = 0.70 in Koster) than in females (m = 0.42 in Hvaler; m = 0.60 in Koster). Reasons for the higher mortality can be that males have lower food intake than females and/or they allocate more energy towards the reproductive activities than females.

A number of studies have reported a trade-off between reproductive effort and adult growth or survival (Gunderson 1997). The spawning season is a challenge to energetic condition and adult mortality is positively correlated with reproductive effort. Luksenburg and Pedersen (2002) found that shorthorn sculpin males had lower growth rates and higher mortality rates compared to females in northern Norway and suggested that the

reproductive effort and natural mortality may be larger in males than in females. The males invest in the reproduction by guarding the eggs of one or two females. Being stationary they are more prone to predation and have less time to feed. In addition, high amounts of sculpin eggs have been observed in cod stomachs during the egg guarding period (Luksenburg et al. 2004). The display behavior of male sculpins may also contribute to the higher mortality: males do not usually avoid other animals, but tries to attack them regardless of the size of the approaching animal in order to protect the eggs or the site where they are located (Ennis 1970a). It is also likely that the males compete for the nest sites and females, which has energy costs. The high mortality rate of males during the egg guarding period has been observed for example in three-spined sticklebacks *Gasterosteus aculeatus* L. (Pressley 1981).

In addition to higher natural mortality, a lack of older males could be due to migration to other regions. But this is not likely because shorthorn sculpin is a stationary species and only migrates to deeper waters during winter (Pethon & Nyström 1998). Only some local migrations may be considered. Finally, selective fishing on larger fishes cannot be the reason for lack of older sculpins, because there is no commercial interest or fishing effort on shorthorn sculpin in Oslofjord.

4.3 Growth

Growth of sculpins in Hvaler and Koster varies between the sexes (Figure 3.5 & 3.6). On average, females became approximately 5 cm longer than males and have approximately identical length growth in Hvaler and Koster (Figure 3.7). Females grow 3.8 cm per year in Hvaler and 3.5 cm per year in Koster. Luksenburg and Pedersen (2002) also found that female sculpins become larger than males in Tromsø. Several other studies have shown that females have quite uniform growth through the life and become larger than males whose growth rate decreases after the age of 2 – 3 (Ennis 1970a; King 1983; Raciborski 1984;

Langvald 2000). The sex-related differences in growth rates of shorthorn sculpins indicate different energy allocation in the two sexes and sexual size dimorphism.

Males from Hvaler were significantly longer than males in Koster, but the difference in length was only about 0.5 cm and therefore has no ecological significance (Figure 3.7). However the growth rates were almost equal: 2.7 cm/year in Hvaler and 2.6 cm/year in Koster. Age explained around 80 % of the variability in length in all cases (Appendix IV). Females grew longer because they lived longer, but the growth rates of both sexes were similar until three years old, when the females became longer (Figure 3.5 & 3.6). Shorthorn sculpins become sexually mature around 3 to 4 years old in Norway (Pethon & Nyström 1998). Males are suggested to have higher reproductive costs which can hinder the energy intake and thus growth. Lower growth rate and higher mortality rate of males compared to females can be consequences of higher reproductive effort and reproductive related mortality in males. Gunderson and Dygert (1988) found that the adult natural mortality rate increased linearly with increasing female reproductive effort (gonad-somatic weight index) in 20 different fish stocks.

Females became significant heavier than males in both areas (Figure 3.8 & 3.9). During the first two years the sexes had approximately the same average weight. At age of 3 females became larger than males. Further, females in Hvaler obtained larger weights than in Koster (Figure 3.10). The observed average weights for 4 year old females were 265 g in Hvaler and 211 g in Koster (although high SD = 65,6 g; Appendix IV). Males from Hvaler were also approximately 6 g heavier than in Koster (Figure 3.10). However, due to a large variability, these differences were not significant.

Based on the mean weights, female sculpins were bigger in Hvaler (150.3 g) than in Koster (101.4 g; Table 3.1). This difference can be due to larger proportion of older females in Hvaler than Koster (Figure 3.1 & 3.2) and/or larger numbers of sealworms in female sculpins in Koster (Table 3.4 & 3.6). High parasite abundances can have negative impact on host growth (Sindermann 1987; des Clers 1990). However, we found almost no

correlation between number of sealworms and weight of the fish in these areas (Figure 3.13 – 3.16). Langvald (2000) observed that females from Hvaler were significantly bigger than females in Koster and she claims that the reason for this could be small local differences in abiotic and biotic factors, which could be the reason in our study as well.

Environmental conditions (i.e. temperature, currents, food availability) are important factors influencing the growth rate and body size of fish (Wootton 1998). The growth of most fish is indeterminate and flexible so that the same species may show different growth in different environments and sexual maturity can be reached at different sizes or ages. There can also be differences in growth between fish born in different years within a population. In addition habitat quality, fecundity and population density influences the growth. Usually fishes in the southern range of the distribution grow faster than in the northern part (Beverton 1992; Luksenburg & Pedersen 2002). This is due to a tendency of warmer waters in southern latitudes, and if food is not a limiting factor, higher temperature increases the metabolic rate and thus growth (Wootton 1998). For example, sculpins in Torbjørnskjær grow faster than in Vega (Andersen 2001). Environmental conditions and habitat type are fairly similar in Hvaler and Koster and that may explain why the two populations had similar growth rates.

4.3.1 Condition of the fish

Length and weight relationships can be used to measure the well being of the fish population (Wootton 1998). Condition may reflect food availability and growth in the weeks prior to sampling, but the average conditions of the population varies seasonally and annually (Schneider et al. 2000). We found no significant difference in the length-weight relationship between the two sexes or between the two areas (Figures 3.23 & 3.24, Appendix I). The condition factor (K) estimated for the different age classes, showed that the females in Hvaler had a slight higher mean condition (K = 1.63, SD = 0.24) than males (K = 1.41, SD = 0.14; Table 3.3). In Koster the sexes had the same condition (females: K =

1.45, SD = 0.18, males: K = 1.46, SD = 0.16). The difference between the regions is not significant. Earlier study from Hvaler and Koster found similar results, where females in Hvaler had better condition (K = 1.6, SD = 0.3), than males (K = 1.4, SD = 0.1) and the sexes had the same condition in Koster (K = 1.5, SD = 0.2) (Langvald 2000). She also found that high parasite number did not have any correlation with the condition of the sculpins. The sculpins in Koster carried higher sealworm burdens than in Hvaler (Table 3.8). However, we found no large difference in the condition between the areas, indicating that the parasite infection do not have any effect on the condition of sculpin in these areas. In Torbørnskjær and Vega the condition factor did not vary with the geographic origin and different sealworm numbers in sculpins (Jensen et al. 1994b).

4.4 Infection rates of the sealworms

The sculpins in Hvaler had a small number of sealworms (0 – 4 sealworms per fish; Appendix II) and the prevalence was low: 27 % of the females and 18 % of the males were infested by sealworms (Table 3.4 & 3.5). In Koster the infection levels were much higher: 87 % of the females and 79 % of the males were infested by sealworms and the number of sealworm per fish varied between 0 and 34 for females with the exception of one highly infected female (102 sealworms; Tables 3.6 & 3.7, Appendix III). The males had less sealworms than females in Koster (0 – 14). On average, the prevalence (fraction infested), abundance (mean worm count in a host sample) and intensity (mean worm count per infected fish) of sealworms in sculpins were higher for females than for males in both areas (Table 3.4 – 3.7). However, these differences between the sexes were not significant (Appendix IV).

The infection levels were higher in Koster, because the sculpins were caught closer to the seal skerries and the abundance of seals is higher. The sealworm egg supply was higher in Koster than in Hvaler, because the sealworms have better changes to reach the final hosts and reproduce than in Hvaler, where the seals are only visiting sporadically the area.

However, the small infection levels in sculpins, which live more than 10 km from the main area of the seals, indicate that the survival in sculpins was high. Experimental studies confirm that sealworms have highest survival in sculpins when transmitted from fish to fish, specifically from sculpin to sculpin (Jensen 1997b). This may also be an important factor why cod from inner Hvaler are practically not infected by *P. decipiens* (Jensen & Idås 1992).

The infection levels found in sculpins in Hvaler in 2009 are very similar to those recorded eleven years earlier in the same location (Langvald 2000). The fraction infested in the whole population was 22 % in 1998 and 24 % in 2009 (Table 3.8). The average abundance was the same (0.4) in both studies and the intensity was 1.7 eleven years earlier and 1.6 in our study (Table 3.8). The infection levels in sculpins did not change in eleven years period in Hvaler, despite the variation in abundance of seals in Torbjørnskjær during this period. The outbreak of the phocine distemper virus (PDV) in European harbour seals in 2002 and in 1988 (Dietz et al. 1989; Jensen et al. 2002) reduced the harbor seal population in Hvaler by about 75 % (Morten Bronndal pers. Comm; Midtgaard et al. 2003). In spite of this fluctuation the infestation in sculpins was nearly identical before and after the outbreak in 2002. This may be due to particular conditions in the Hvaler area. The rate of sealworm infections in fish is usually positively correlated with abundance of seals in the area (McCelland et al. 1983; Jensen et al. 1994a). However, it seems that the abundance of sealworms in sculpin is independent of the number of seals in the area when the number of seals is over a certain threshold (Jensen et al. 1994b; Lunneryd et al. 2001).

Much higher infection levels (prevalence 80.8 %, abundance 36.1) than in this study was recorded in the sculpins caught from the shallow waters around the seal skerries in Torbjørnskjær in 1991 – 1992 (Jensen et al. 1994a). The prevalence was similar to Koster (85 % infested; Table 3.8), where the seal population is three times larger. But the average abundance (36.1) was much higher than in Koster (6.4; Table 3.8). However the high abundance observed in Hvaler can be due to one extremely infected sculpin with 411 sealworms. In addition, Andersen (2001) found high total abundances of sealworms (19.47

– 57.22) in sculpins from the shallow waters around Torbjørnskjær islands between 1991 and 1996. Again few individuals were heavily infected (with maximum 424 sealworms) and these infection levels in sculpins were higher than reported elsewhere (Lamp 1966; Ennis 1970a; Háuksson 1992; Kerstan 1992; Jensen et al. 1994a; Aspholm et al. 1995).

At Torbjørnskjær there is a smaller number of haul-out skerries, thus the seal density and infection levels in fish are locally high around the skerries. This is why several fish hosts have much lower infection levels slightly outside the seal skerries in Torbjørnskjær (Jensen et al. 1994a). Furthermore, the infection levels in sculpins are much higher in Torbjørnskjær than in Vega, which has a larger number but smaller density of seals (Andersen 2001). This is because Vega has 6500 islands and skerries, so the seals and the sealworm eggs in faeces are dispersed over a much larger area than in Torbjørnskjær (Jensen et al. 1994a). In addition, there are grey seals in Vega that tend to migrate and disperse over larger area than harbour seals. The differences in the diet of sculpins also contribute to the differences in the infection levels. For example, at Torbjørnskjær sculpins eat more amphipods than in Vega (Andersen 2001) and amphipods are very common invertebrate hosts for *P. decipiens* (McClelland 1990).

An increase in infection rates has been observed in some species when the diet changes from benthic to piscivorous as the fish matures (McCelland et al. 1990; Jensen et al. 1994b; Andersen 2001). In the Sable Island the diet of Atlantic cod changed as the fish matured. While the diet of younger individuals is dominated by benthic invertebrates, the older prefer a variety of fish and this change is followed by a dramatic increase in prevalence and abundance of the sealworm *P.decipiens* (McCelland et al. 1990). A change in diet has also been observed in sculpins in Torbjørnskjær, where the type of prey changed from amphipods (90 % of the diet in juveniles) to decapods (14 %), amphipods (29 %) and fish (41 %) as the sculpins became older and larger (Jensen et al. 1994b). The fish prey included sculpins, cod and butterfish (*Pholis gunnellus*). Consequently the change in diet was followed by larger sealworm numbers.

4.5 Infection levels in relation to age and size of fish

A larger fraction of females than males was infested (Table 3.4 – 3.7). One reason may be that females tend to be larger and older than males. The infection levels are assumed to increase with increasing age and size of the host within a population (des Clers 1989; Jensen et al. 1994b; McClelland 2002). Older and larger fish have a larger consumption and is therefore likely to encounter more infested prey. Platt (1975) and des Clers (1989) claimed that sealworm abundance is more related to host size than age. In addition that they have been longer time exposed to possible infected prey populations. In sculpins from Torbjørnskjær and Vega the increase in infection level with fish length and age was evident (Jensen et al. 1994b).

We found almost no correlation between the number of sealworms and weight of the fish (Figure 3.13 – 3.16). In Koster there was a small correlation between weight and sealworm burden in female sculpins (Figure 3.15). Weight explained 17 % of the variation in sealworm numbers in female sculpin. However, because of the non-random distribution of sealworms in sculpins in Koster (Figure 3.19 – 3.22) some of the sculpins had heavy sealworm infections by chance, while others had only few sealworms. The increasing infection with age in Koster (Table 3.4 & 3.6) may be due to large isolated abundances of sealworms that allows accumulation in older fish. A small population of sealworms in Hvaler did not sustain accumulation of sealworms in older and heavier individuals.

4.6 Distribution of sealworms in fish

The parasite populations are controlled by birth, death and immigration processes (Anderson & Gordon 1982). These factors tend to produce greater variability in parasite numbers in a host than those simply controlled by immigration and death processes. In the case of *Pseudoterranova decipiens* the hatching of the eggs (birth) are dependent on the sea temperature and oxygen availability (Measures 1996). Long periods of low water

temperatures (0°C) decrease the probability of hatching as the temperatures increase. In addition the probability of transmission (infection) increases when the hosts are abundant and at a susceptible age or size.

If the size of the parasite population is mainly controlled by immigration (infection) and death processes (natural mortality or mortality of the host) the parasite abundance in hosts will approximately have a Poisson distribution provided that the mortality rate of the host is independent of the parasite burden (Anderson & Gordon 1982). However, often due to environmental stochasticity such patterns are rarely observed in nature and the distribution of the parasite in a host population tends to be overdispersed.

The number of sealworms per fish had a Poisson distribution in both sexes in Hvaler (Figures 3.17 & 3.18), but exhibited a large deviation from the Poisson distribution in Koster (Figures 3.19 – 3.22). The sealworms were randomly distributed within the sculpin population in Hvaler and overdispersed in Koster. In Hvaler the immigration and death rates seemed to be constant in time and between hosts, leading to a Poisson distribution of sealworms in sculpins. Random distribution of sealworms can lead to a reduction in the reproduction success of the parasite, because a low density of conspecifics translates into a lower probability of the sealworms to reach the final host and mature (Luong et al. 2011). The immigration of sealworms to sculpins is a direct entrance via food. When sculpins feed at random on invertebrates and fish the distribution of sealworms will be random in the population. A random feeding means that the proportion of prey in the diet equals its proportion in the environment (Lechowicz 1982). However if each host populations in the food chain feeds on the infected prey at random the distribution of the sealworm gets overdispersed in the end (Ronald 1989).

In Koster a high consistent abundance of seals induce a large population of sealworms and a high consistent infection rate in hosts. Therefore the infection level is high in sculpins in Koster and varies by chance between the individuals with few extremely infected sculpins.

This creates over-dispersed distribution of sealworms in sculpin in Koster. In Hvaler the immigration of sealworms to sculpins is dependent on harbour seals visiting the area. These seals transport sealworms of which a significant fraction is acquired from a different population of sculpins or other intermediate hosts from the area around the Torbjørnskjær Islands, where the infection levels are higher.

At Torbjørnskjær young sculpins feed mainly on amphipods, while the older prey on fish (Jensen et al. 1994b). Therefore, the random distribution of sealworms in sculpins in Inner Hvaler (Figure 3.17 & 3.18) may to some extent be explained by a geographic variation in the diet. Similarly, heterogeneity in fish behavior may generate the overdispersion, which was observed in Koster (Anderson et al. 1978; Anderson & Gordon 1982). Sculpins seem to have different food preferences in Inner Hvaler and Koster. The foraging behavior of sculpins defines the actual transmission level of sealworms to next host.

The vast majority of parasites exhibit an aggregated distribution in the host population and, as in Hvaler, most of the hosts have few or no parasites, while only a minority of hosts are heavily infected (Luong et al. 2011). High numbers of parasites in a host can result in increased mortality of the parasite and parasite-induced host mortality, when the infection level in population increases. This was earlier considered to be the reason for high mortality rates in Koster (Females M = 0.91, males M = 1.19; Table 3.2). However, the reduction in the infection levels in older individuals may also be induced by parasite-induced mortality (Anderson & Gordon 1982). The opposite pattern was found in Koster, where the infection rate increased towards the older age classes (Table 3.6 & 3.7). If the host death rate is positively correlated with the parasite burden the distribution of parasites within the host population tend to be underdispersed (Anderson & Gordon 1982). However, it has been difficult to demonstrate the parasite-induced host mortality in the field, mainly because dead hosts are rarely found, and if they are, the cause of death is difficult to measure (Gordon & Rau 1982; Scott & Dobson 1989; Rousset et al. 1996).

4.5 Conclusions

Female shorthorn sculpins may live one year longer and grow larger than males. A plausible explanation for the smaller growth rate and higher mortality rate of males is that they allocate more energy on reproductive activities. Females in Koster experienced a higher mortality (lower age) than females in Hvaler, and this difference may perhaps be linked to a larger parasite burdens. There were no significant differences in the growth rate between Hvaler and Koster, which is likely due to similar habitat type.

The sculpins in Koster had high sealworm burdens, which is a result of a high consistent abundance of seals in the Koster archipelago. Long distance from the seal skerries and random visits of the harbour seals resulted in a small sealworm infection rate in the inner Hvaler. The sealworm burden did not have any measurable effect on the condition of sculpin in these areas.

On average, there was no correlation between the number of sealworms and weight of the fish. In Koster there was a small correlation between weight and sealworm burden in female sculpins. Furthermore, older females had higher infection levels than younger females in Koster. This is due to large isolated abundances of sealworms that allows accumulation in older fish. However, because of the non-random distribution of sealworms in sculpins some of the fish had heavy sealworm infections by chance, while others had only few sealworms. A small population of sealworms in Hvaler did not sustain accumulation of sealworms in older and heavier individuals.

The number of sealworms in sculpins had a random distribution (Poisson) in Hvaler and overdispersed (not symmetric around the average parasite burden) in Koster. Different feeding preferences and diet of sculpins in Hvaler and Koster could partly explain the different distribution. In Inner Hvaler the sculpins feed randomly on a variety of types of prey with a generalist strategy.

Heterogeneity in the feeding behavior and the difference in seal abundance between Koster and Hvaler may explain the difference in distribution of sealworms in sculpins between the areas. However, further studies are needed to describe the relationship between diet and parasite burden of sculpins in the outer Oslofjord.

4.6 Future research

Still little is known about the biology of shorthorn sculpin in Norway. Several studies have shown geographical variation in life history parameters (Lamp 1966; Ennis 1970b; King 1983; Luksenburg & Pedersen 2002) and sealworm abundances between the populations of shorthorn sculpins (Jensen et al. 1994a; Langvald 2000; Andersen 2001). But only few studies have shown variation in infection levels with age and size of sculpin (Jensen et al. 1994a; Andersen 2001). We found no significant correlations between the number of sealworms and weight and age of the fish (Figure 3.13 – 3.16). Further studies would be needed to clarify the relationship between infection levels and age and size of fish. Also larger sample size would be needed in order to investigate a possible increase in infection levels in older individuals (in our study the oldest individuals were only 4.5 years old).

As the rate of accumulation of sealworms may reflect growth rate of the fish and infection levels in previous hosts (des Clers 1989) the type of prey becomes important in the transmission of sealworms to fish. Studies on invertebrates in areas with high sealworm abundance could provide information on the early part of the sealworm life-cycle. In addition a further study should investigate the stomach contents of sculpins from Hvaler and Koster and describe the diet. An experimental study on food preferences in relation to sealworm numbers in sculpins could reveal important aspects of the feeding behavior. Further studies should put emphasis on the feeding behavior of sculpins and other infected fish in relation to sealworm numbers in fish and abundance of seals. Diet and food preferences seem to play an important role in the distribution of sealworms in fish.

Many studies have been concentrating on sealworm abundances in commercial fish such as cod. This study revealed for a first time a random distribution of sealworms in sculpins in Hvaler (Figure 3.17 & 3.18). Thus it would be useful to investigate the distribution of sealworms in other highly infected demersal fish in order to reveal the factors causing different distribution of parasites in fish.

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Personal comments

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Appendix I

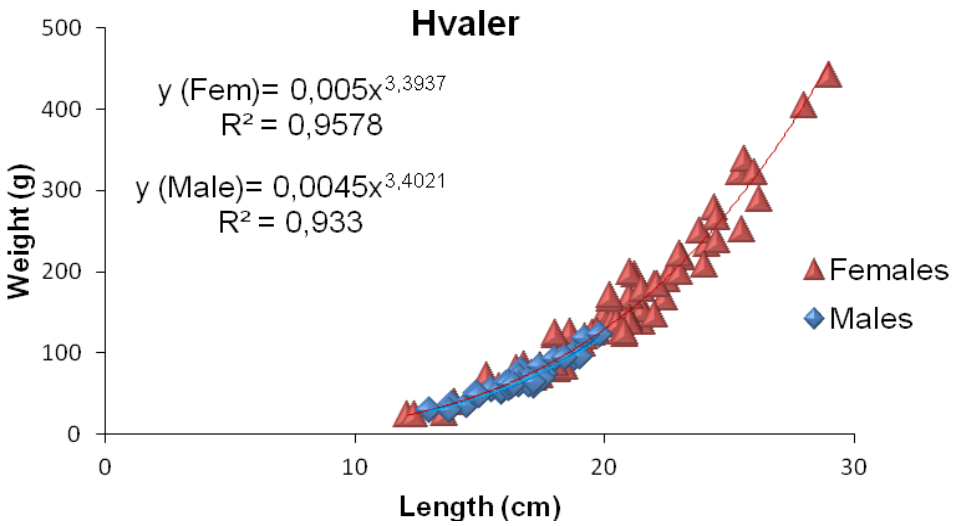

Figure 3.23 Weight versus length for sculpins from Hvaler.

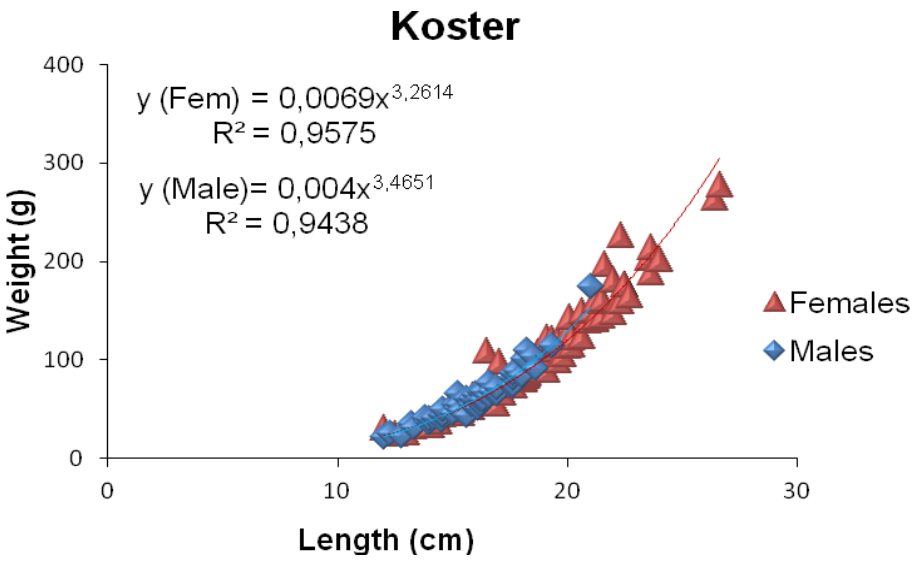

Figure 3.24 Weight versus length for sculpins from Koster.

Appendix II

Biological data (sex, age, length in cm, weight in grams) of sculpins (*Myoxocephalus scorpius*) from the Hvaler Islands and the number of third stage sealworm larvae (*Pseudoterranova decipiens*) in their fillets. These data are ordered into 12 tables according to sex, sampling place and date.

Table A1. n = 16 female sculpins sampled in Asmaløy (Hvaler, Norway) on 6 September 2009.

Asmaløy 6 September 2009

sex	AGE	Length (cm)	Weight (g)	Pd
f	1.5	12.1	23	0
f	2.5	15.3	71	0
f	2.5	15.8	58	0
f	2.5	16.5	80	0
f	2.5	17.1	69	1
f	2.5	17.4	83	0
f	2.5	17.4	84	0
f	3.5	18.1	79	0
f	3.5	18.4	82	0
f	3.5	19.1	111	0
f	3.5	19.2	120	0
f	3.5	20	148	0
f	3.5	21	137	0
f	3.5	21.3	167	0
f	4.5	22.4	168	2
f	4.5	24.1	233	2

Table A2. n = 13 female sculpins sampled in Asmaløy (Hvaler, Norway) on 13 September 2009.

Asmaløy 13 September 2009

sex	AGE	Length (cm)	Weight (g)	Pd
f	1.5	13.6	25	0
f	2.5	16.8	66	0
f	2.5	16.8	85	0
f	3.5	18.6	126	0
f	3.5	19.5	124	0
f	3.5	20.1	135	0
f	3.5	20.3	139	0
f	3.5	20.5	137	0
f	3.5	20.8	143	0
f	3.5	21.5	137	0
f	3.5	21.5	153	4
f	3.5	22	147	2
f	4.5	23.1	216	0

Table A3. n = 5 female sculpins sampled in Asmaløy (Hvaler, Norway) on 23 September 2009.

Asmaløy 23 September 2009

sex	AGE	Length (cm)	Weight (g)	Pd
f	1.5	14	39	2
f	3.5	21	169	1
f	3.5	21.2	195	0
f	4.5	25.4	321	1
f	4.5	29	441	0

Table A4. n = 14 female sculpins sampled in Kirkøy (Hvaler, Norway) on 8 September 2009.

Kirkøy 8 September 2009

sex	AGE	Length (cm)	Weight (g)	Pd
f	1.5	12.4	23	0
f	2.5	16.5	66	1
f	2.5	16.7	75	1
f	2.5	17.1	74	0
f	2.5	18	86	1
f	3.5	20.5	138	0
f	3.5	21	142	0
f	3.5	21	199	3
f	3.5	22	183	1
f	4.5	22.5	189	0
f	4.5	23.8	249	0
f	4.5	24.5	237	0
f	4.5	25.6	338	1
f	4.5	26.2	289	0

Table A5. n = 17 female sculpins sampled in Kirkøy (Hvaler, Norway) on 19 September 2009.

Kirkøy 19 September 2009

sex	AGE	Length (cm)	Weight (g)	Pd
f	1.5	14	38	0
f	2.5	16.8	68	0
f	2.5	17.1	68	1
f	2.5	17.4	72	0
f	3.5	19.7	125	3
f	3.5	20.2	166	1
f	3.5	20.2	171	0
f	3.5	21	138	0
f	3.5	21.5	178	1
f	3.5	22.1	183	0
f	4.5	22.7	199	0
f	4.5	23	199	0
f	4.5	24	208	3
f	4.5	24.4	278	0
f	4.5	25.5	251	0
f	4.5	26	321	0
f	4.5	28	404	0

Table A6. n = 9 female sculpins sampled in Kirkøy (Hvaler, Norway) on 27 September 2009.

Kirkøy 27 September 2009

sex	AGE	Length (cm)	Weight (g)	Pd
f	2.5	17.2	68	0
f	2.5	17.3	78	1
f	3.5	18	121	0
f	3.5	18	124	0
f	3.5	20.7	126	0
f	3.5	20.8	123	0
f	3.5	20.8	126	0
f	4.5	23	221	0
f	4.5	24.5	266	0

Table A7. n = 7 male sculpins sampled in Asmaløy (Hvaler, Norway) on 6 September 2009.

Asmaløy 6 September 2009

sex	AGE	Length (cm)	Weight (g)	Pd
m	1.5	13	29	0
m	2.5	15.5	55	0
m	2.5	15.9	52	0
m	2.5	16.1	62	0
m	2.5	17.2	60	0
m	3.5	18.8	100	0
m	3.5	19.2	118	1

Table A8. n = 4 male sculpins sampled in Asmaløy (Hvaler, Norway) on 13 September 2009.

Asmaløy 13 September 2009

sex	AGE	Length (cm)	Weight (g)	Pd
m	1.5	13.9	37	0
m	2.5	16.7	79	0
m	2.5	17.5	77	0
m	3.5	18.8	94	0

Table A9. n = 4 male sculpins sampled in Asmaløy (Hvaler, Norway) on 13 September 2009.

Asmaløy 23 September 2009

sex	AGE	Length (cm)	Weight (g)	Pd
m	2.5	14.9	51	0
m	2.5	17.5	71	1

Table A10. n = 6 male sculpins sampled in Kirkøy (Hvaler, Norway) on 8 September 2009.

Kirkøy 8 September 2009

sex	AGE	Length (cm)	Weight (g)	Pd
m	1.5	14.5	35	0
m	2.5	15.9	53	0
m	2.5	16.6	72	0
m	2.5	17.1	70	4
m	2.5	17.6	74	0
m	3.5	19	96	0

Table A11. n = 10 male sculpins sampled in Kirkøy (Hvaler, Norway) on 19 September 2009.

Kirkøy 19 September 2009

sex	AGE	Length (cm)	Weight (g)	Pd
m	2.5	14.9	47	1
m	2.5	15	48	1
m	2.5	16.2	57	0
m	2.5	16.2	62	0
m	2.5	16.6	61	0
m	2.5	17	61	0
m	2.5	17.4	84	0
m	2.5	17.5	69	0
m	3.5	18	92	0
m	3.5	19.8	123	0

Table A12. n = 4 male sculpins sampled in Kirkøy (Hvaler, Norway) on 27 September 2009.

Kirkøy 27 September 2009

sex	AGE	Length (cm)	Weight (g)	Pd
m	1.5	13.8	30	0
m	2.5	16.4	61	0
m	2.5	17.2	64	0
m	3.5	18.4	94	1

Appendix III

Biological data (sex, age, length in cm, weight in grams) of sculpins (*Myoxocephalus scorpius*) from the Koster Archipelagos and the number of third stage larvae of seal worms (*Pseudoterranova decipiens*) in their fillets. These data are ordered into 2 tables according to sex.

Table A13. n = 109 female sculpins sampled in the Koster archipelago (Sweden) during the 1990's in August – October.

sex	AGE	Length (cm)	Weight (g)	Pd
f	1.5	12	30	6
f	1.5	12.5	24	0
f	1.5	13	25	16
f	1.5	13.3	31	2
f	1.5	13.7	35	3
f	1.5	14	39	2
f	1.5	14.1	33	2
f	1.5	14.4	36	0
f	1.5	14.6	43	3
f	1.5	14.6	44	1
f	1.5	14.8	47	4
f	2.5	15	45	1
f	2.5	15	48	1
f	2.5	15.2	50	0
f	2.5	15.3	57	4
f	2.5	15.4	45	2
f	2.5	15.4	48	7
f	2.5	15.5	53	1
f	2.5	15.5	54	0
f	2.5	15.8	51	0
f	2.5	15.9	56	0
f	2.5	15.9	63	0
f	2.5	16	64	1

Table A13 Continued. n = 109 female sculpins sampled in the Koster archipelago (Sweden) during the 1990's in August – October.

sex	AGE	Length (cm)	Weight (g)	Pd
f	2.5	16.1	60	6
f	2.5	16.2	63	0
f	2.5	16.4	55	8
f	2.5	16.5	55	3
f	2.5	16.5	56	2
f	2.5	16.5	108	2
f	2.5	16.6	60	4
f	2.5	16.7	66	0
f	2.5	16.9	55	3
f	2.5	16.9	69	2
f	2.5	17	97	1
f	2.5	17.1	66	1
f	2.5	17.2	66	0
f	2.5	17.4	78	7
f	2.5	17.5	73	4
f	2.5	17.5	73	2
f	2.5	17.6	73	7
f	2.5	17.6	80	1
f	2.5	17.6	82	12
f	2.5	17.7	73	4
f	2.5	17.8	94	8
f	2.5	17.9	81	8
f	2.5	18	85	1
f	2.5	18.1	79	4
f	2.5	18.1	82	0
f	2.5	18.1	85	6
f	2.5	18.1	98	5
f	2.5	18.2	83	1
f	2.5	18.2	90	17
f	2.5	18.2	91	15

Table A13 Continued. n = 109 female sculpins sampled in the Koster archipelago (Sweden) during the 1990's in August – October.

sex	AGE	Length (cm)	Weight (g)	Pd
f	2.5	18.3	85	3
f	2.5	18.3	88	1
f	2.5	18.4	89	12
f	2.5	18.4	96	22
f	2.5	18.5	92	9
f	2.5	18.6	97	7
f	2.5	18.6	99	3
f	3.5	18.6	102	9
f	3.5	18.7	101	2
f	3.5	18.7	107	3
f	3.5	18.9	99	4
f	3.5	18.9	99	13
f	3.5	19	105	0
f	3.5	19	107	3
f	3.5	19.1	89	0
f	3.5	19.1	100	8
f	3.5	19.1	101	11
f	3.5	19.1	122	28
f	3.5	19.3	109	13
f	3.5	19.3	115	0
f	3.5	19.3	121	6
f	3.5	19.6	99	15
f	3.5	19.6	118	5
f	3.5	19.8	105	4
f	3.5	20	113	14
f	3.5	20	127	1
f	3.5	20.1	143	4
f	3.5	20.2	114	12
f	3.5	20.2	122	7
f	3.5	20.6	123	8

Table A13 Continued. n = 109 female sculpins sampled in the Koster archipelago (Sweden) during the 1990's in August – October.

sex	AGE	Length (cm)	Weight (g)	Pd
f	3.5	20.6	149	12
f	3.5	20.9	139	10
f	3.5	21	149	10
f	3.5	21	149	13
f	3.5	21	150	19
f	3.5	21.2	140	6
f	3.5	21.2	143	8
f	3.5	21.2	160	2
f	3.5	21.5	144	13
f	3.5	21.5	159	102
f	3.5	21.5	161	17
f	3.5	21.6	196	12
f	3.5	22	147	6
f	3.5	22	181	21
f	3.5	22.2	160	4
f	3.5	22.3	158	27
f	3.5	22.3	226	5
f	3.5	22.5	175	14
f	4.5	22.5	175	9
f	4.5	22.7	164	6
f	4.5	23.5	203	3
f	4.5	23.6	188	10
f	4.5	23.6	213	23
f	4.5	24	201	14
f	4.5	26.4	263	34
f	4.5	26.6	277	10

Table A14. n = 52 male sculpins sampled in the Koster archipelago (Sweden) during the 1990's in August – October.

sex	AGE	Length (cm)	Weight (g)	Pd
m	1.5	12	21	0
m	1.5	12.3	25	7
m	1.5	12.8	23	2
m	1.5	13.2	35	0
m	1.5	13.3	31	2
m	1.5	13.8	41	3
m	1.5	13.9	37	0
m	1.5	14	36	7
m	1.5	14	40	1
m	2.5	14.2	41	0
m	2.5	14.5	38	0
m	2.5	14.5	43	14
m	2.5	14.6	44	4
m	2.5	14.6	49	1
m	2.5	15	46	1
m	2.5	15.1	55	3
m	2.5	15.2	51	8
m	2.5	15.2	66	3
m	2.5	15.3	54	5
m	2.5	15.4	48	1
m	2.5	15.6	44	4
m	2.5	15.6	61	6
m	2.5	15.8	55	2
m	2.5	15.8	61	6
m	2.5	16	57	1
m	2.5	16	60	0
m	2.5	16	64	0
m	2.5	16.1	51	4
m	2.5	16.1	58	4
m	2.5	16.1	58	6

Table A14 Continued. n = 52 male sculpins sampled in the Koster archipelago (Sweden) during the 1990's in August – October.

m	**2.5**	**16.2**	**54**	**0**
m	**2.5**	**16.2**	**59**	**2**
m	**2.5**	**16.2**	**67**	**8**
m	**2.5**	**16.3**	**59**	**3**
m	**2.5**	**16.3**	**68**	**0**
m	**2.5**	**16.6**	**63**	**1**
m	**2.5**	**16.6**	**76**	**1**
m	**2.5**	**16.7**	**68**	**6**
m	**2.5**	**16.9**	**66**	**0**
m	**2.5**	**16.9**	**72**	**1**
m	**2.5**	**17.5**	**74**	**6**
m	**2.5**	**17.6**	**74**	**3**
m	**3.5**	**17.6**	**81**	**4**
m	**3.5**	**17.6**	**86**	**8**
m	**3.5**	**17.8**	**89**	**7**
m	**3.5**	**18**	**84**	**13**
m	**3.5**	**18.1**	**101**	**6**
m	**3.5**	**18.2**	**109**	**0**
m	**3.5**	**18.5**	**103**	**6**
m	**3.5**	**18.6**	**91**	**13**
m	**3.5**	**19.3**	**114**	**7**
m	**3.5**	**21**	**174**	**6**

Appendix IV

Statistical tests

Table A15. Age distribution. Females versus males in Hvaler. Chi-square test.

	Age 1.5	Age 2.5	Age 3.5	Age 4.5	Total
Hvaler Females	5	17	33	19	74
Hvaler Males	4	22	7	0	33
Total	9	39	40	19	107
Age distribution	0.0841	0.3645	0.3738	0.1776	1.0000

Expected under H0	Age 1.5	Age 2.5	Age 3.5	Age 4.5	Total
Hvaler Females	6	27	28	13	74
Hvaler Males	3	12	12	6	33
	9	39	40	19	107
	0.24	3.69	1.03	2.61	
	0.54	8.27	2.31	5.86	
	CHI =	24.55			
	DF =	3			
	P =	0.000			

Table A16. Age distribution. Females versus males in Koster. Chi-square test.

	Age 1.5	Age 2.5	Age 3.5	Age 4.5	Total
Koster Females	11	49	41	8	109
Koster Males	9	33	10	0	52
Total	20	82	51	8	161
Age distribution	0.1242	0.5093	0.3168	0.0497	1.0000

Expected under H0	Age 1.5	Age 2.5	Age 3.5	Age 4.5	Total
Koster Females	14	56	35	5	109
Koster Males	6	26	16	3	52
	20	82	51	8	161
	0.48	0.76	1.21	1.23	
	1.00	1.60	2.54	2.58	
	CHI =	11.42			
	DF =	3			
	P =	0.010			

Table A17. Age distribution of females. Hvaler versus Koster Chi-square test.

	Age 1.5	Age 2.5	Age 3.5	Age 4.5	Total
Hvaler Females	5	17	33	19	74
Koster Females	11	49	41	8	109
Total	16	66	74	27	183
Age distribution	0.0874	0.3607	0.4044	0.1475	1.0000

Expected under H0	Age 1.5	Age 2.5	Age 3.5	Age 4.5	Total
Hvaler Females	6	27	30	11	74
Koster Females	10	39	44	16	109
	16	66	74	27	183
	0.33	3.52	0.32	5.98	
	0.23	2.39	0.21	4.06	
	CHI =	17.04			
	DF =	3			
	P =	0.001			

Table A18. Age distribution of males. Hvaler versus Koster Chi-square test.

	Age 1.5	Age 2.5	Age 3.5	Age 4.5	Total
Hvaler Males	4	22	7	0	33
Koster Males	9	33	10	0	52
Total	13	55	17	0	85
Age distribution	0.1529	0.6471	0.2000	0.0000	1.0000

Expected under H0	Age 1.5	Age 2.5	Age 3.5	Age 4.5	Total
Hvaler Males	5	21	7	0	33
Koster Males	8	34	10	0	52
	13	55	17	0	85
	0.22	0.02	0.02	0.00	
	0.14	0.01	0.02	0.00	
	CHI =	0.43			
	DF =	2			
	P =	0.808			

Table A19. Length versus age. Hvaler. Linear Regression

Females

Source	SS	df	MS	F	P	crit
Regression	797.3	1	797.3	492	0.000	3.97
Residual	116.713	72	1.621			
Total	914.0	73				

R^2	0.8723
s^2 Y;X	1.27
sb	0.17

Males

Source	SS	df	MS	F	P	crit
Regression	66.9	1	66.9	107	0.000	4.16
Residual	19.421	31	0.626			
Total	86.3	32				

R^2	0.7750
s^2 Y;X	0.79
sb	0.24

H0: b1 = b2

W RSS =	1.322
s b1-b2 =	0.384
t =	3.402
df =	103
t 0.05; df =	1.98
P =	0.001

Table A20. Length versus age. Koster. Linear Regression

Females

Source	SS	df	MS	F	P	crit
Regression	743.0	1	743.0	550	0.000	3.93
Residual	144.7	107	1.352			
Total	887.7	108				

R^2	0.8370
s^2 Y;X	1.16
sb	0.14

Males

Source	SS	df	MS	F	P	crit
Regression	129.1	1	129.1	174	0.000	4.03
Residual	37.1	50	0.743			
Total	166.2	51				

R^2	0.7765
s^2 Y;X	0.86
sb	0.20

H0: b1 = b2

W RSS =	1.158
s b1-b2 =	0.281
t =	2.789
df =	157
t 0.05; df =	1.98
P =	0.006

Table A21. Weight versus length. Hvaler. Log-Transformed. Linear Regression

Females

Source	SS	df	MS	F	P	crit
Regression	27.7	1	27.7	1633	0.000	3.97
Residual	1.221	72	0.017			
Total	28.9	73				

R^2	0.96
s^2 Y;X	0.13
sb	0.08

Males

Source	SS	df	MS	F	P	crit
Regression	3.8	1	3.8	432	0.000	4.16
Residual	0.270	31	0.009			
Total	4.0	32				

R^2	0.93
s^2 Y;X	0.09
sb	0.16

H0: b1 = b2

W RSS =	0.014
s b1-b2 =	0.225
t =	-0.037
df =	103
t 0.05; df =	1.98
P =	0.970

Table A22. Weight versus length. Koster. Log-Transformed. Linear Regression

Females

Source	SS	df	MS	F	P	crit
Regression	28.2	1	28.2	2410	0.000	3.93
Residual	1.3	107	0.012			
Total	29.5	108				

R^2	0.96
s^2 Y;X	0.11
sb	0.07

Males

Source	SS	df	MS	F	P	crit
Regression	8.0	1	8.0	839	0.000	4.03
Residual	0.5	50	0.010			
Total	8.5	51				

R^2	0.94
s^2 Y;X	0.10
sb	0.12

H0: b1 = b2

W RSS =	0.011
s b1-b2 =	0.144
t =	-1.416
df =	157
t 0.05; df =	1.98
P =	0.159

Table A23. Weight versus age. Hvaler. Polynomial Regression

Hvaler	Females		Hvaler	Males	
	LINEAR			LINEAR	
a	-137.84		a	-21.0	
b1	84.938		b1	35.7	
R sq	0.7279		R sq	0.8025	
SS RES	148684.071		SS RES	3776	
	QUADRATIC			QUADRATIC	
a	64.438		a	5.0	
b1	-51.373		b1	13.7	
b2	21.23		b2	4.4	
R sq	0.7734		R sq	0.8105	
SS RES	123844		SS RES	3659	
n	74		n	33	
a	-137.8	64.4	a	-21.01	4.9545
b1	84.9	-51.4	b1	35.66	13.683
b2		21.2	b2		4.4075
SS Res	148684	123844	SS Res	3776	3659
df		71	df		30
F		14	F		0.956
P		0.000	P		0.336
Quadratic sign			Quadratic not sign		

Table A24. Weight versus age. Koster. Polynomial Regression

Koster	Females		Koster	Males	
	LINEAR			LINEAR	
a	-67.9		a	-28.4	
b1	58.0		b1	35.9	
R sq	0.76		R sq	0.68	
SS RES	69250		SS RES	11619	
	QUADRATIC			QUADRATIC	
a	15.483		a	-28.364	
b1	-2.6583		b1	35.877	
b2	10.262		b2	0.000	
R sq	0.7809		R sq	0.6777	
SS RES	62702		SS RES	11619	
n	109		n	52	
a	-67.926	15.483	a	-28.364	-28.364
b1	57.953	-2.6583	b1	35.877	35.877
b2		10.262	b2		0.000
SS Res	69250	62702	SS Res	11619	11619
df		106	df		49
F		11	F		0.000
P		0.001	P		1.000
Quadratic sign			Quadratic not sign		

Table A25. Weight of 4.5 year old females. Hvaler versus Koster. t-test.

	Females	
	Hvaler	**Koster**
n =	**19**	**8**
sum Y =	**5028**	**1684**
Av Y =	**265**	**211**
sum YY =	**1426952**	**365742**
(n-1)*s ^2 =	**96384**	**11260**
SS Tot	**107644**	
df	**25**	
MS Tot	**4306**	
s combined	**65.6**	
s difference	**27.7**	
t =	**1.96**	
P =	**0.062**	

Table A26. Weight of 4.5 year old females. Hvaler versus Koster. t-test.

HVALER Males

Source	SS	df	MS	F	P	crit
Regression	13642	1	13642.0	126	0.000	4.16
Residual	3357	31	108.289			
Total	16999	32				

R^2	0.80
s^2 Y;X	10.41
sb	3.18

KOSTER MALES

Source	SS	df	MS	F	P	crit
Regression	24432	1	24431.8	105	0.000	4.03
Residual	11619	50	232.383			
Total	36051	51				

R^2	0.68
s^2 Y;X	15.24
sb	3.50

H0: b1 = b2

W RSS =	184.890
s b1-b2 =	5.194
t =	-0.042
df =	81
t 0.05; df =	1.99
P =	0.967

H0: a1 = a2

Ac = xx 1 +xx 2	29.7
Bc = xy 1 + xy 2	1063.5
Cc = yy 1 + yy 2	53049.9
SS c = C - B^2 / A	14976.4
DF c = n1 + n2 - 3	82
s^2 = MS c = SS/DF	182.6
b c = xy/xx	35.80
(Y1-Y2)-b(X1-X2)	3.23
s^2(1/n1+1/n2 + (X1-X2)^2/A)	9.08
sqrt()	3.01
T	1.073
P	0.286

Table A27. Prevalence of females versus males in Hvaler. Chi-square test.

HVALER

	Infected	Not Infected	Total
Hvaler Females	20	54	74
Hvaler Males	6	27	33
Total	26	81	107

	p infected	p not infected
	0.243	0.757

Expected under H0	Infected	Not Infected	
Hvaler Females	18	56.0	74
Hvaler Males	8	25	33

	0.23	0.07
	0.51	0.16
CHI =		0.97
P =		0.32

Table A28. Prevalence of females versus males in Koster. Chi-square test.

KOSTER

	Infected	Not Infected	Total
Koster Females	95	14	109
Koster Males	41	11	52
Total	136	25	161

	p infected	p not infected
	0.845	0.155

Expected under H0	Infected	Not Infected	
Koster Females	92.1	16.9	109
Koster Males	44	8	52

	0.09	0.51
	0.19	1.06
CHI =		1.85
P =		0.17